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BULLETIN OF MARINE SCIENCE OF THE GULF AND CARIBBEAN

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The Seasonal Distribution of Oceanic Birds in the Western North Atlantic¹

HILARY B. MOORE

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For a number of years a log has been kept on the Woods Hole Oceanographic Institution vessel *Atlantis* of all birds seen at sea. This recording, which was initiated by Dr. A. C. Redfield, has largely been carried out by Chief Engineer Harold Backus, but a considerable body of data has also been contributed by Dr. Redfield, Alfred H. Woodcock, Dean F. Bumpus, Frank J. Mather III and others. A similar record has been kept by the author for the Bermuda area and during several North Atlantic transects, and some of this has already been published (Moore 1941). Dr. E. F. Thompson and Miss K. S. Russell assisted with these. Redfield (1941) has published those of his observations which were relevant to the Gulf of Maine.

The literature has been so well covered by Wynne-Edwards (1935) and Murphy (1936) that there is no need to refer to it in detail; it is sufficient to quote from their summaries. They make it plain that at present we know only the broad outlines of the migration routes and seasons for oceanic birds, and that more observations are urgently needed. The present paper covers only a small portion of the North Atlantic, but the fairly considerable body of data affords the opportunity for a more detailed analysis of seasonal distribution than has previously been possible. In order to utilize as much as possible of the data, certain restrictions have had to be made. While some of the records specify numbers of birds seen per hour of observation, others give only numbers per day, so it has been necessary to reduce them all to the latter basis. We have also restricted the paper to include only the area for which there is adequate coverage at all seasons. The logs

1. Contribution No. 560 from Woods Hole Oceanographic Institution.
Contribution No. 48 from Marine Laboratory, University of Miami.

include also some data from more extended cruises, and many observations on littoral birds such as gulls and on migrant land birds encountered at sea.

The fact that the records have been made by different observers presents a difficulty. All were reasonably well acquainted with the birds in question, but we are dealing almost entirely with sight records, and some errors must be assumed to have occurred. Where the identifications may be in doubt, this is discussed under the section on species in question. Observations were not made continuously all day, but any birds sighted by others were usually reported to the person keeping the records. Somewhat lower population figures may therefore be expected than those obtained from continuous observations such as Wynne-Edwards made, but the overall picture of distributions is not likely to be false. Where a flock of birds such as petrels has followed the ship throughout the day and been logged a number of times, the largest number logged has been taken as the total for the day. While this may be too low, it avoids multiple recording of the same birds.

The author was responsible for only a small fraction of the observations, and wishes to acknowledge the much greater share of credit due to those who have been collecting them for so many years. Thanks are also due to Dr. Redfield, Mr. Bumpus and others who have assisted with the preparation of the paper. The original logs are filed at the Woods Hole Oceanographic Institution.

The data are given on the accompanying maps as numbers of each species seen per day. For the shearwaters and petrels the information has been grouped as a monthly average for each five-degree square, and the number of days on which observations were made is indicated. For the less frequent records of phalaropes and jaegers, total numbers recorded for each month are shown, and these are grouped in two periods covering the spring and fall migrations respectively. Reference to Figures 1 and 2 will show the number of days of observations. Seasonal coverage is not complete in the southern part of the area, but fortunately it is adequate for the winter and spring when the north-bound migrants are most likely to be found there. The grouping of the data by months will result in some masking of the exact dates of the advancing waves of migration, but this would have occurred anyhow as a result of our grouping together data from many different years. For simplicity, the number of days of observation are shown only in Figures 1 and 2, but the same values are applicable for all species.

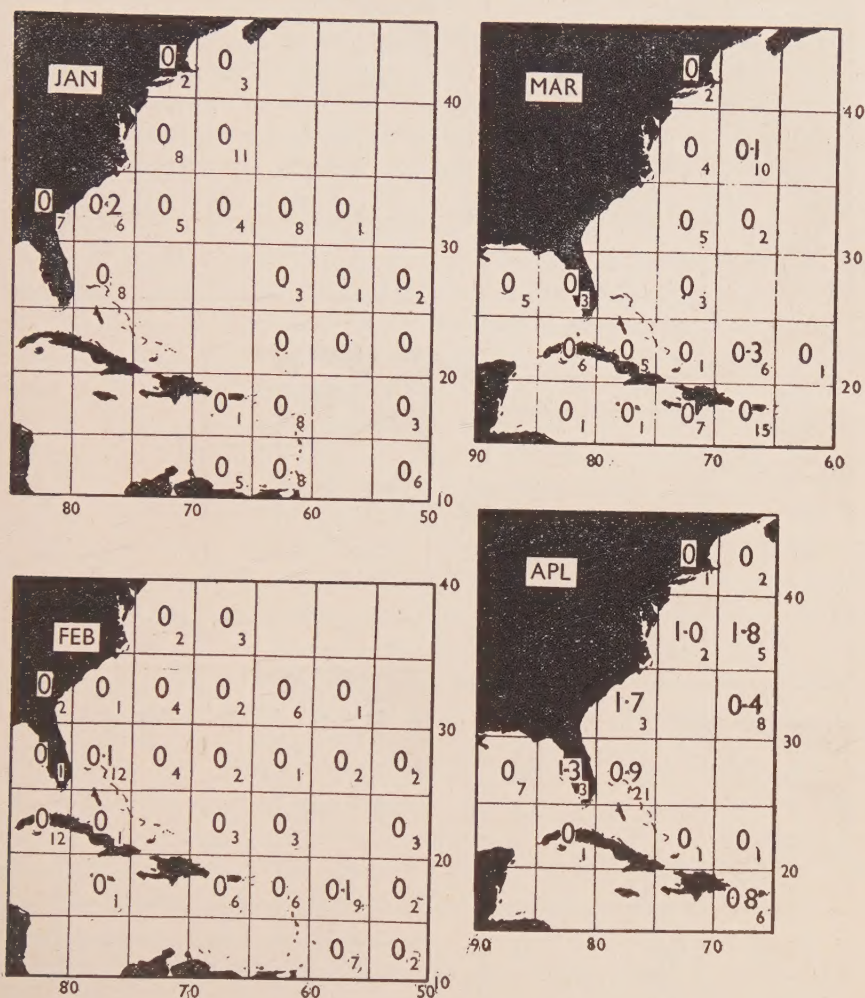


FIGURE 1

FIGURES 1 & 2. Wilson's Petrel. Average numbers seen per day in each five-degree square. The suffixes indicate the number of days of observation in that square during the month (i.e., 1.7₁₀ indicates a total of 17 birds seen in 10 days, or an average of 1.7 per day). No observations are available for the blank squares.

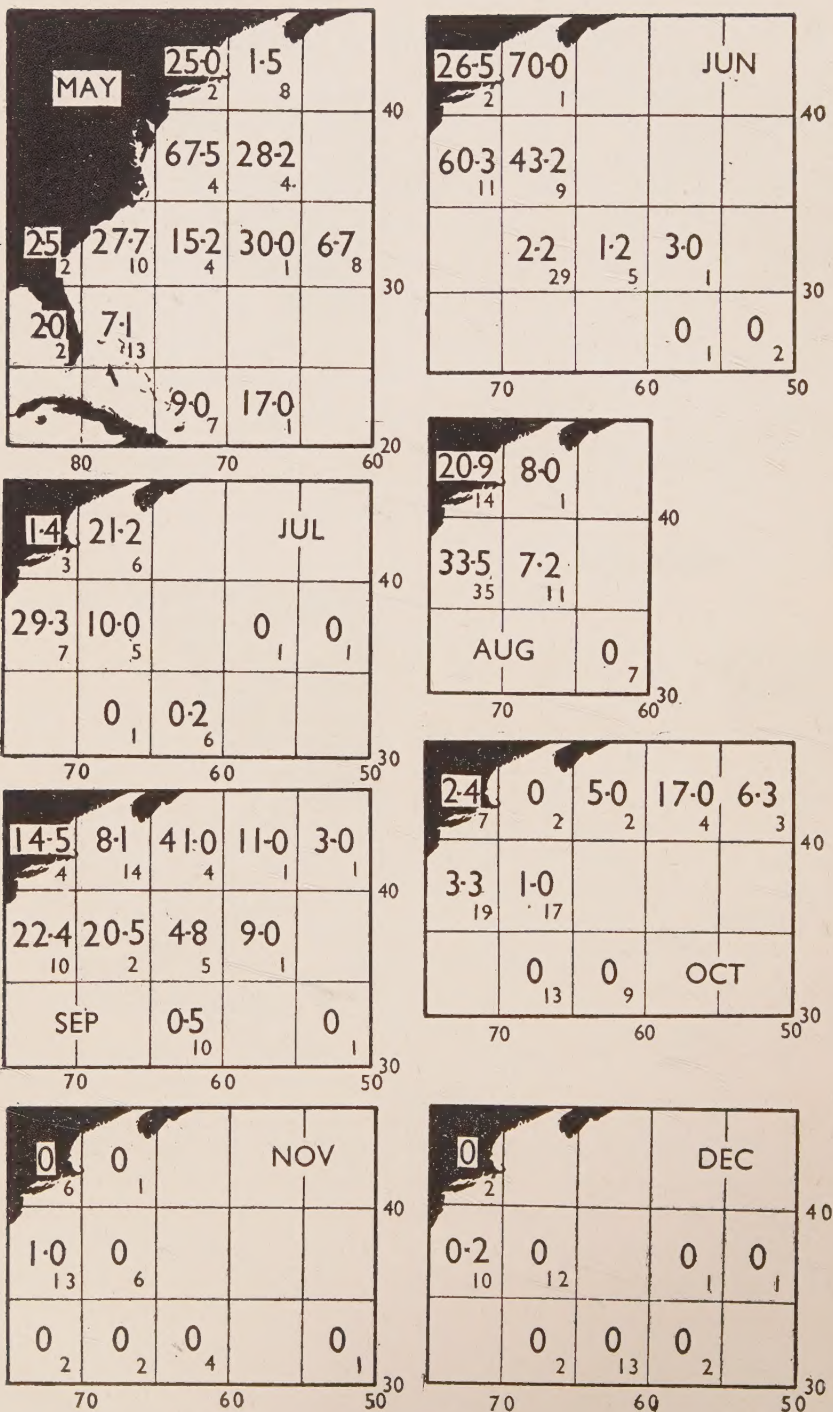


FIGURE 2

WILSON'S PETREL, *Oceanites oceanicus* (Kuhl). Figs. 1 and 2.

Wilson's petrel breeds in the Antarctic, arriving at the breeding grounds in November (Murphy 1936). Wynne-Edwards (1935) states that there are North Atlantic records for all months except February, and that there would appear to be a considerable non-breeding population of immature birds. Our records from December to March are so few that the birds may be said to be virtually absent from the area, although there are single records for all months. The few storm petrels seen in these months were probably Wilson's, but there is some room for doubts in the identification. Wynne-Edwards shows that they appear in the Sargasso Sea in increasing numbers throughout April, and along the North American coast in the later half of that month. He also points out their greater concentration along the Gulf Stream than elsewhere in the open ocean. Our records show them in small numbers in April along the east coast and just inside the Gulf of Mexico. Redfield (1941), whose results are incorporated with ours, found them absent at that time from the Gulf of Maine. Maximum numbers for the area as a whole were attained in May, and there was a definite concentration in and near the Gulf Stream, although they were still abundant further seawards. Numbers were about the same in June, but the concentration had moved north and shorewards, and there was a decrease in the Bermuda area. In the Gulf of Maine, numbers were small in May, and maximum from June to September. For the area as a whole, numbers dropped somewhat in July, August and September, and in the latter month there was indication of decreasing numbers along the coast and a spread seawards to the north-east along the line of the Gulf Stream. By October there was a marked drop in numbers, and the main concentration was along the line of the Gulf Stream at about 55° to 60° N., and by November practically all birds had left the area.

LEACH'S PETREL, *Oceanodroma leucorhoa* (Viellot). Figs. 3 and 4.

Definite identifications as Leach's petrel may be taken as correct, but it may be that some of the records of Wilson's petrels should have been referred to this species. Even allowing for this possibility, there is no doubt that Leach's is much the rarer species in the area. Redfield found not more than one to twenty or thirty Wilson's petrels in the Gulf of Maine.

Leach's petrel nests in the northern part of the area, and according to Wynne-Edwards and Murphy is more or less restricted during the

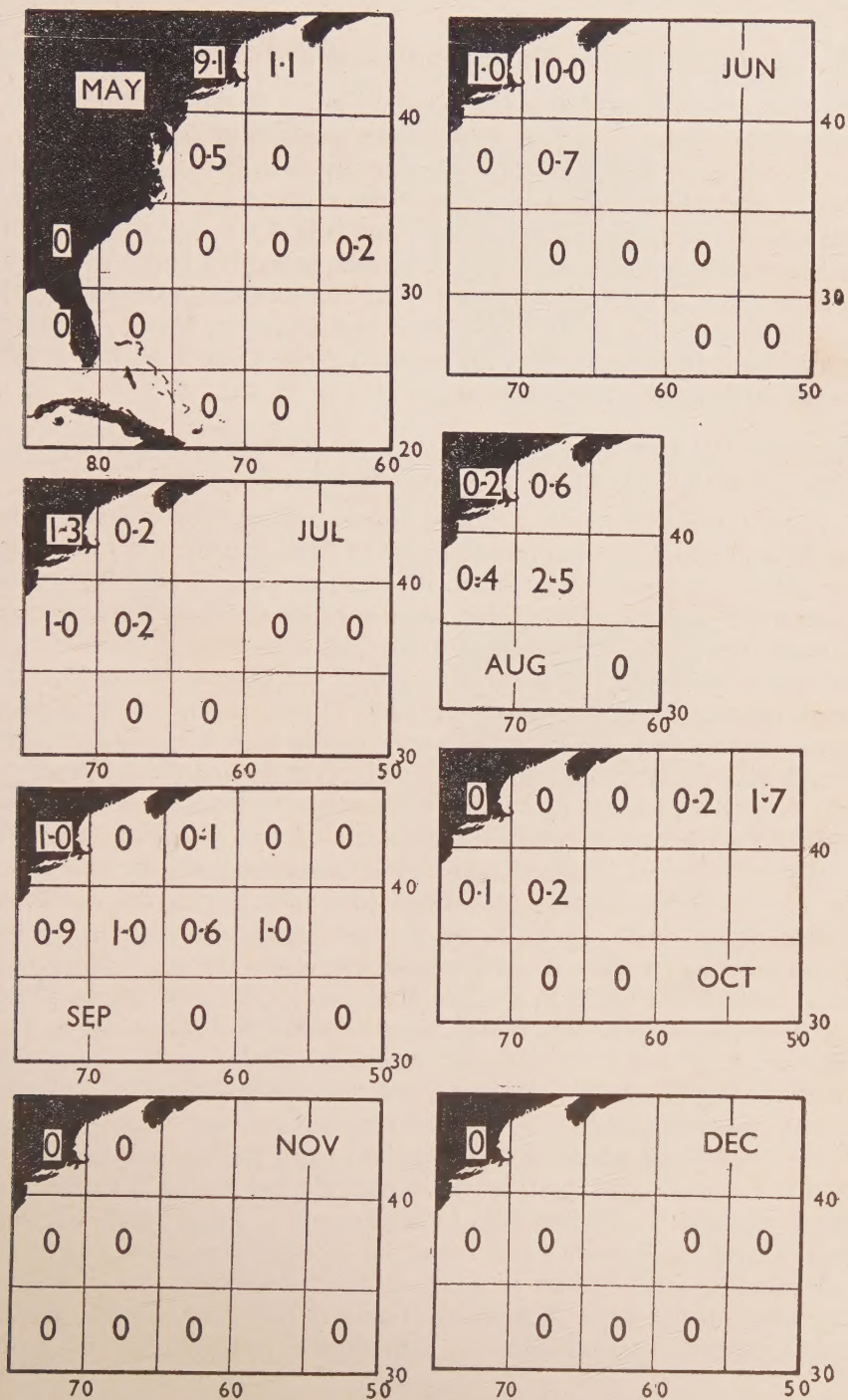


FIGURE 4

breeding season to within a few hundred miles of the nesting site. It winters far south, arrives on its northern grounds in April and May, and moves south again in September and October. From November to March, our only records were a few in the extreme south in February. The next record is near the breeding grounds in April, and they did not become common there until May. Numbers remained about the same in June, after which they dropped, and there was some evidence of an offshore movement in September and October. Mather reports that in both 1948 and 1949, all petrels seen in Cape Cod Bay from August to September were Wilson's.

GREAT SHEARWATER, *Puffinus gravis* (O'Reilly). NORTH ATLANTIC SHEARWATER, *P. kuhlii* (Boie). Figs. 5 and 6.

These two species were confused in our earlier observations, so it seems better to consider them together at first, and then see how far the records can be distinguished. The sub-species *P. kuhlii borealis* Cory and *P. kuhlii kuhlii* (Boie) were not distinguished. Our records showed them practically absent from the area from December to February, and present in small numbers off the West Indies in March. Small numbers were seen along the Gulf Stream in the southern part of the area in April, and further north, and in somewhat larger numbers in May and June. Numbers dropped markedly in July and August, and then in September rose much higher than in the spring. They remained high in October, and in the Cape Cod area into November.

Wynne-Edwards shows that the great shearwater, which breeds in the central South Atlantic at Tristan da Cunha during the northern winter, moves north rapidly in the northern spring, passing Cape Cod about the end of May. It then spreads eastwards during the summer and moves south again in the fall, the return migration taking place partly on the western, but mainly on the eastern side of the Atlantic. On the other hand, the North Atlantic shearwaters breed on the European coasts during the northern summer, and, according to Wynne Edwards, spread westwards across the Atlantic between July and October. They occur from Cape Hatteras to Cape Cod from the end of August to November, and move south for the winter. Except during the southerly fall migration, the distributions of *P. kuhlii* and *P. gravis* hardly overlap on the American coast. There seems little doubt that the first peak in our records, from March to May or June, represents the northerly migration of the great shearwater. Those of our later records, where the two species were satisfactorily distinguished, support this. We have

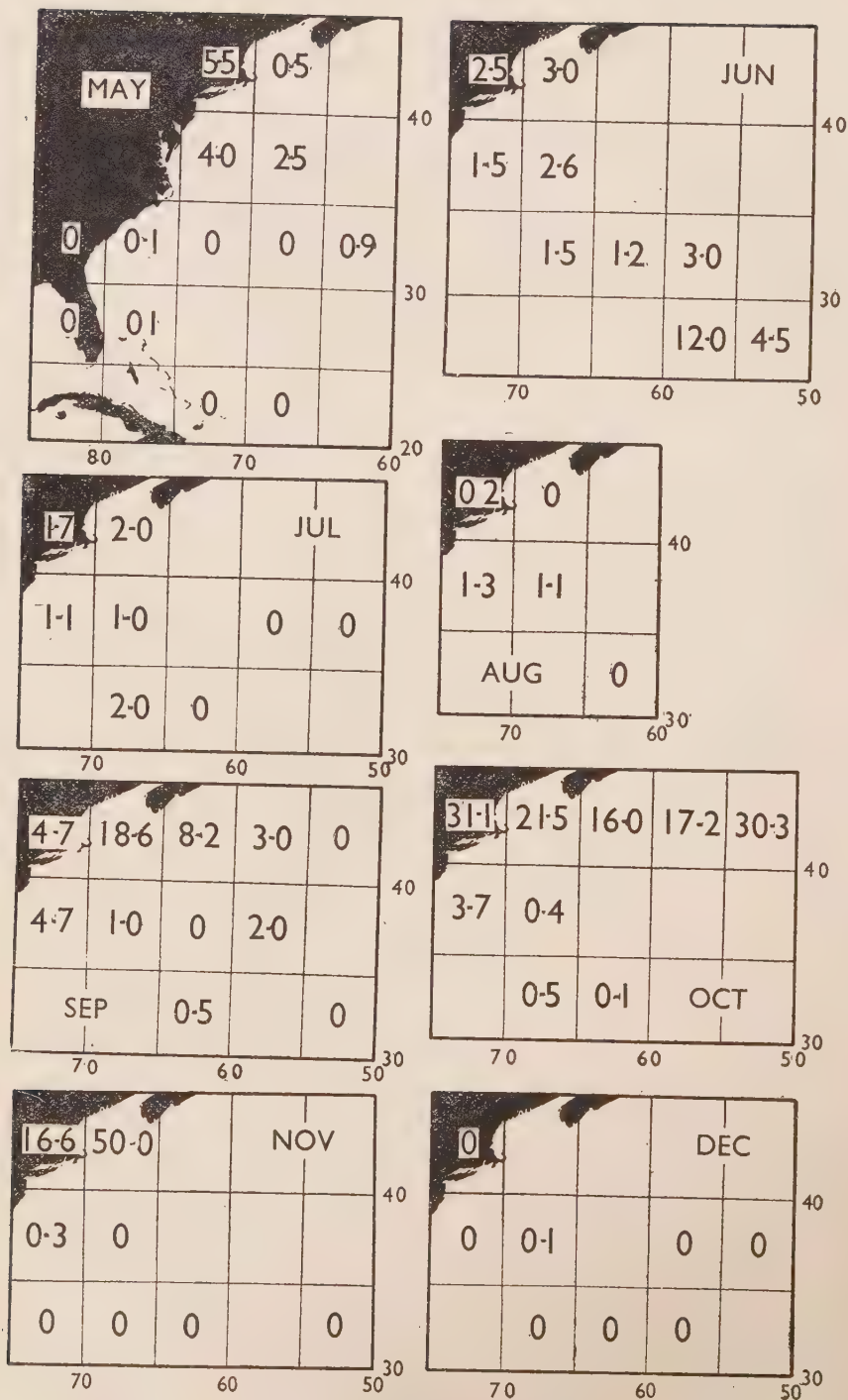


FIGURE 6

a single record of three Atlantic shearwaters off Bermuda on May 28 (Moore 1941), and one of a single bird between Bermuda and Cape Cod in mid-June. Mather (*in litt.*) observed considerable numbers of large shearwaters in Cape Cod Bay, and all of those which could be specifically identified in June 1949 were great shearwaters, while all those from July 25 to October 17, 1948 were Atlantic shearwaters. From this it would appear that Atlantic shearwaters must reach the American coasts somewhat earlier than Wynne-Edwards suggests, and while the European breeding season is still at its height. Wynne-Edwards indicates the return migration of the great shearwater as passing through our area in September-October, so presumably the second peak in our records, which occurs at this period, represents a mixture of the two species. Unfortunately, the records are not adequate to show which species predominates.

The unsatisfactory nature of these results is obvious, but the scarcity of other oceanic records for the area justifies their publication in this form.

NORTHERN PHALAROPE, *Lobipes lobatus* (Linn.). **RED PHALAROPE**, *Phalaropus fulicarius* (Linn.). Fig. 7.

It is rarely possible to distinguish the species of phalaropes at sea, and only two of our records make a definite identification of red phalaropes. Both of these were in September, and between Cape Cod and 150 miles south of there. The rest of the records are entered as northern

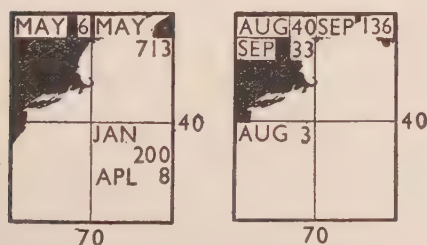


FIGURE 7. Phalaropes. Total numbers recorded (for details, see text). Comparison with Figures 1 & 2 will show the extent of the area from which none were recorded.

phalaropes, and this is probably a correct identification of most of them. Both species nest in the Arctic, and make a spring and fall migration through the area. On the spring migration northwards we have one record of a flock seen in January, one in April, and all the rest in May. A record of Redfield's, not included on the chart, is that of about five hundred phalaropes, in small flocks, all flying east by north, between

Browns Bank and Cape Sable on May 28, 1934. All our fall records were in August and September.

Our observations agree well with what is already known of phalarope migrations. The surprising thing about them is the fact that none were ever seen outside a very limited region. Comparison with the charts for shearwaters or petrels will show how large an area of the ocean was covered during their migration season without any being sighted. It is true that they are inconspicuous and easily missed, but this hardly seems to be an adequate explanation of the lack of records. There is still much to be learned with regard to both their wintering

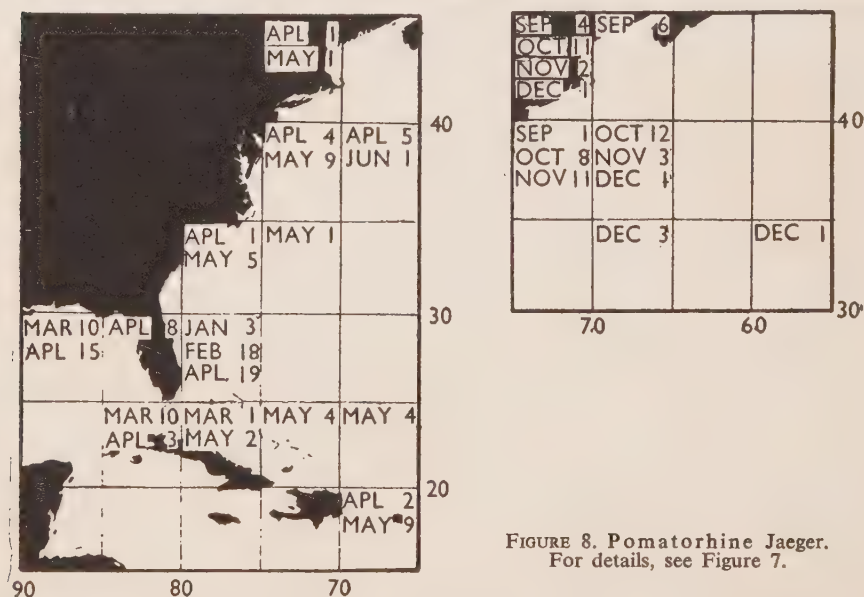


FIGURE 8. *Pomatorhine Jaeger*.
For details, see Figure 7.

grounds and how they reach them, and our records do little to clarify these questions. They might perhaps lend support to the possibility that most of the migration is overland, or alternatively that, when at sea, they migrate mainly at night. In the latter case, if they were resting on the water during the daytime, they might well escape observation.

POMATORRHINE JAEGER, *Stercorarius pomarinus* (Temminck).
Fig 8.

The comparatively few jaeger records are, like the petrel records, shown individually and in two groups covering the spring and fall migrations respectively. In the spring, a few pomatorhine jaegers were

seen as early as January at 29°N., and rather more in February in the Florida—West Indies area. In March and April they were seen all through this area and along the northern part of the Gulf of Mexico. Since there was no opportunity for observation in the Gulf before March, we have no evidence as to whether any of the birds winter there: it is clear, however, that there is a considerable concentration of pomatorhine jaegers in the Gulf of Mexico—West Indies area in the spring, and some time before they appear off the New England coast. Wynne-Edwards records them on the northern grounds at the end of April and beginning of May. Our records agree with this, our latest record being one bird seen in June.

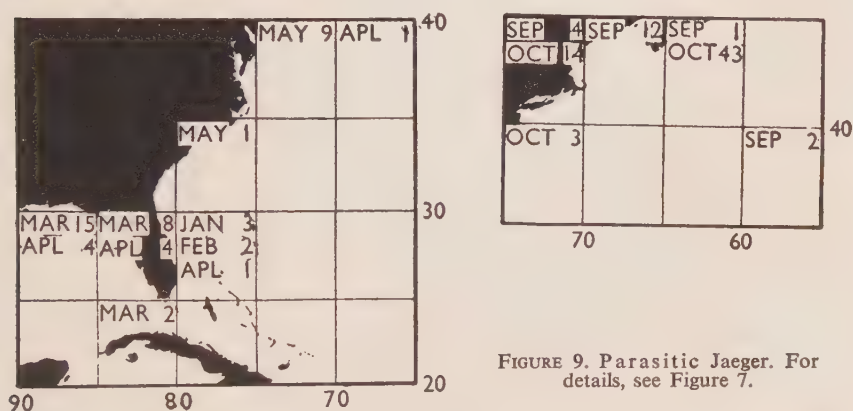


FIGURE 9. Parasitic Jaeger. For details, see Figure 7.

Records for the fall migration are strongly concentrated in the region of the Gulf Stream at about 40°N., and ranging from September to December. Wynne-Edwards saw his first birds of the season there in mid-August. The southern part of the area is less well covered by observations in the fall than in the spring, but the fact that the few November and December records were to the southeast suggests the possibility of the fall migration lying more to seaward than the spring one.

PARASITIC JAEGER, *Stercorarius parasiticus* (Linn.). Fig. 9.

There are fewer records of this species than of the pomatorhine jaeger, but, as far as the spring migration is concerned, they are very similar. A few were seen in January and February in the Florida—West Indies area, and more in March and April in the northern Gulf of Mexico. By May they appeared to be moving north along the coast. Again there is no additional evidence of their winter status in the Gulf.

Fall records were restricted to September and October, whereas pomatorhine jaegers were seen as late as December. Their locations were all between about 40 and 45°N., and there was a tendency to spread further seawards, and to do this at a more northerly latitude, than in the last species. This would agree with Wynne-Edwards' opinion that the parasitic jaeger is a more oceanic bird than the pomatorhine.

LONG-TAILED JAEGER, *Stercorarius longicaudus* Viellot Fig. 10.

This species was considerably less common than the last. Its distribution, both spring and fall, was the same, except that the earliest spring record was in March. Wynne-Edwards describes it as a still more oceanic migrant than the parasitic jaeger.

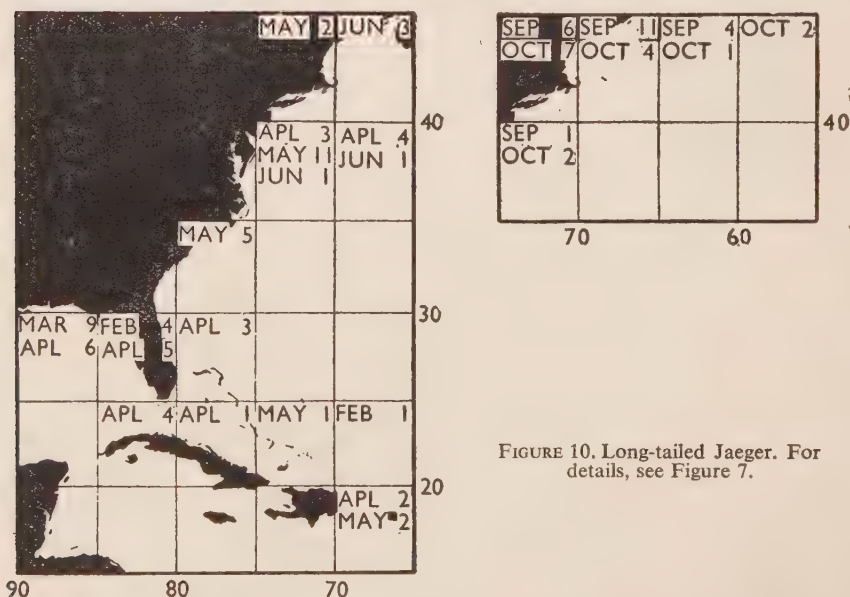


FIGURE 10. Long-tailed Jaeger. For details, see Figure 7.

MOORE, H. B.

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The Morphology of *Balanus improvisus* Darwin and *Balanus amphitrite niveus* Darwin During Initial Attachment and Metamorphosis¹

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The morphology of the Cirripedia has received considerable attention since the proper systematic position of the group was established upon discovery of the nauplius stage by Thompson (1830). Most of the studies, however, have been of gross anatomy, which does not provide the detailed information given by microsections. Hoek (1884) sectioned adults and described the anatomy of a cypris from crude longitudinal sections. Groom (1894) sectioned nauplii, but no other records have been found of similar treatment of cyprids.

Among the Cirripedia are free-living and parasitic forms without the slightest resemblance to each other as adults, having only the six nauplius and single cypris stages in common. The close similarity of the larval stages is in marked contrast to the wide divergence of form and mode of life of the adults. Because of this similarity, a study of the larvae of any cirripede is a useful aid to comprehension of the entire group. With regard to fouling of ships' bottoms, the most important phase of development is the metamorphosis from cypris to adult, for at this point in their life history barnacles abandon the free-swimming planktonic life to become sessile.

Because of the dearth of detailed information about stages immediately following attachment, the present study was initiated. Especial attention was paid to examination of sections as well as to observations on living cyprids.

The writer wishes to express his sincere appreciation to F. G. Walton Smith for suggesting the problem, for guidance during the course of his study and for reading the manuscript.

HISTORICAL SUMMARY

The cypris larva was first described by Burmeister (1834), shortly after discovery of the nauplius stage by Thompson. Burmeister presented the first anatomical account of any importance, but also added

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to the confusion of some later workers. Unaware of the metanauplius stage with its rudimentary six pairs of swimming appendages, he described an intermediate stage with a bivalve carapace and three pairs of appendages. He based his description on a single specimen. Nothing similar has since been found.

The two-volume monograph by Darwin (1851-54) is unequalled in scope by other studies of the Cirripedia. His discussion includes morphology, ecology and taxonomy.

The value of Claus' (1869) account of the cypris and its metamorphosis was increased by his studies on other Entomostraca. His is the only detailed account of the period immediately following attachment, but it is based entirely on whole mounts and dissections of the appendages. Without knowledge of the metanauplius, he suspected the existence of another stage between the nauplius as he knew it, and the cypris. His careful dissections added materially to Darwin's observations and led him to suggest that the intermediate stage of Burmeister was erroneous.

Descriptive embryology of the cypris stage has since been more specific, and has dealt with the development of specific structures such as the mouth parts (Groom, 1895b), plates (Runnstrom, 1925), and eyes (Fales, 1928). Two papers describe cyprids of different species for purposes of identification (Nilsson-Cantell, 1921 and Pyefinch, 1948a).

Since 1928 studies of cirripede larval stages have mainly referred to the general biological, ecological and physiological aspects of species which are most important in fouling.

Observations on the behavior and metamorphosis of living cyprids have been reported by Burmeister (1834), Darwin (1851), Hesse (1874), Willemoes-Suhm (1876), Fales (1928), Visscher (1928), Bohart (1929), Herz (1933) and Pyefinch (1948b), among others. Except for Bohart, all agree for the most part, although no account covers the subject in any great detail. The metamorphosis which Bohart reported in *Balanus crenatus* and *B. glandula* was radically different from that of any other barnacles known, and differs from that reported by Herz for the first named species. In her account there was no exuviation; the cypris merely widened along a dorsal ridge, "increased in depth below the valves to form a gelatinous ring and thus became sessile." The valves of the cyprid carapace then developed into the opercular valves.

MATERIALS AND METHODS

Balanus improvisus Darwin, *B. amphitrite niveus* Darwin and *B. eburneus* Gould are the dominant fouling organisms in Biscayne Bay. Of the three species, the cyprids of *B. eburneus* occur in the smallest numbers, and for this reason the study was limited to *B. improvisus* and *B. amphitrite*. Although these forms may be found at any time of the year, each has distinct seasonal peaks (Weiss, 1948) when numbers sufficient for study are obtainable.

No effort was made to distinguish cyprids by species before attachment, since, within an hour after cementing themselves to the substrate, they assume a characteristic shape by which they may be readily identified (Fig. 1). This is contrary to the statement by Visscher and Luce (1928) that these species may be distinguished only by the presence of certain granules in the carapace. The cypris of *Balanus improvisus* is cigar-like, the width at each end the same, whereas that of *B. amphitrite* is much broader at the anterior end than at the posterior. The ends of the former are conspicuously notched, while the valves of the carapace of the latter come into contact at their apices, or with a very slight notch at the anterior end. The shape of the anterior end of *B. amphitrite* is somewhat variable, and may be merely bluntly rounded or almost as broad as the width at the compound eyes; such a cypris would be nearly triangular.

Measurements of several dozen individuals of both species showed an accompanying size difference. The average length of the cyprids of *Balanus amphitrite niveus* was 534 μ , while that of *B. improvisus* was 587 μ . The average width is 249 μ for the former, and 269 μ for the latter. These distinctions have no great statistical significance because of the variation, so that they do not constitute a safe method of diagnosis.

Collections were made from plankton tows and from small rafts holding glass slides. Wooden panels were fitted with grooved strips into which the slides were inserted; these were floated with the slides on the underside of the panel. This side was painted black to attract the photonegative larvae.

Larvae were fixed in alcoholic seawater Bouin's or in 10% formalin, and preserved in 85% alcohol. Heavy *in toto* staining with fast green was followed by embedding in paraffin. Material was sectioned transversely, sagittally and frontally from 9 μ to 15 μ . Sections were then stained with Ehrlich's acid haematoxylin. Fast green persisted only in the extruded cement and heavier chitin. Whole mounts were left un-

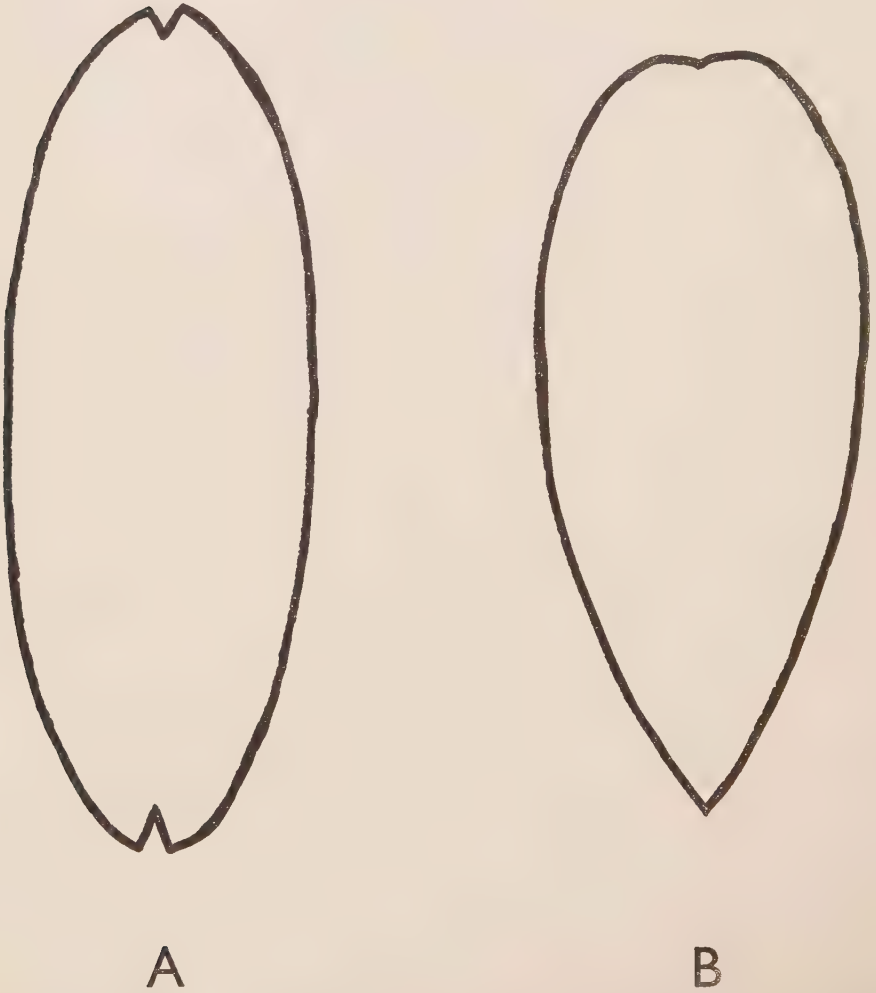


FIGURE 1. Shape of carapace, dorsal aspect, in (A) *Balanus improvisus* and (B) *B. amphitrite niveus*.

stained or stained with Delafield's haematoxylin, Ehrlich's acid haematoxylin, Grenacher's borax carmine, and Ranvier's picro-carmin. The last named gave the most useful results.

Studies on living larvae were made in the winter of 1946-47, and in the summer of 1947. Slides removed from the floating panels were immediately examined under the microscope. There was no loss of larvae in transferring the slides since they adhered so strongly to the glass that unattached cyprids were often found creeping over the surface. These could be removed with a pipette, but once attachment was established by means of the cement, the strongest jet of water from a pipette could not dislodge them. These forms were carefully scraped off. Attached larvae could be observed easily in both dorsal and ventral views and, with some difficulty, from the side.

Attachment to freshly exposed slides was rare, and best results were obtained on surfaces exposed long enough to become covered with a slime film. The necessity of a slime film for barnacle attachment has been studied since 1923 by a score of investigators. The subject is thoroughly discussed by Miller, Rapean and Whedon (1948), who conclude that a bacterial film, although not necessary for the attachment of larvae, may facilitate it. Glass itself is not an attractive surface, as demonstrated by Pomerat and Weiss (1946). A microporous substratum is preferred, and many more cyprids settled upon the wooden float than upon the slides.

Tidal movements influenced settling in a definite way. The greatest numbers of cyprids were invariably taken on the outgoing tide. Indeed, the ebb tide was the only time that proved practical for the collection of larvae before attachment. This observation agrees with those of Visscher (1928a) and Weiss (1947).

OBSERVATIONS ON THE LIVING CYPRIDS

The creeping period before attachment was as long as ten minutes, but there was no way of knowing how long the larva had quit its planktonic existence before examination. In several cases it left the slide to swim about freely, using the thoracic appendages. In contrast to this, the uneven creeping movements were carried out by the large prehensile antennae.

The movements of the cypris have not heretofore been reported and will therefore be discussed in detail. Upon location of a suitable place (having no apparent difference from many places at which it had paused before), final attachment was made following several turns in

which the antennal suction discs were used as pivots. The rotations were produced by the swimming appendages. 360° or more at first, they decreased in both extent and frequency, and after five minutes were short twists of less than 90° . The latter continued for fifteen minutes. They decreased gradually in scope and were accompanied by occasional hindward thrusts of the thoracic appendages. Within twenty-five minutes after attachment all outward movement ceased until just before ecdysis, except for a barely perceptible tilting of the hind end of the body.

When first attached, the cypris was quite transparent, but became more and more opaque until, finally, only the eyes, heavily pigmented areas, stomach, and some oil globules could be discerned.

Before the animal became completely opaque, segmentation of the thorax, individual joints of the appendages, caudal fork, and numerous opaque, yellowish-white granules in the postero-lateral mantle folds were easily distinguished. The paired compound eyes and median nauplian eye were even more conspicuous. Anterior to these was a considerable mass of oily parenchyma forming a pair of bilaterally arranged, disc-shaped areas which twisted periodically in a horizontal plane, each disc moving independently. This was the only movement anterior to the eyes. It occurred irregularly from the time of attachment to that of ecdysis.

The region behind the eyes moved as a unit with the thorax and its appendages. The movement of this unit in relation to the surrounding corium every few seconds was especially prominent during settling, and the first half hour thereafter. Rate of movement was irregular, and at times occurred as often as once per second. As the central body mass was drawn anteriorly, the surrounding posterior half of the corium moved backwards. On return of the central mass to its original position, the corium was simultaneously drawn forward.

The granules in the corium became invisible with increasing opacity, and the thoracic appendages were obscured. The sliding movement of the central body mass and corium decreased in rate until, at ecdysis, it occurred about once per minute. The large brown food body was clearly visible behind the median eye. During the early, transparent stage, the lumen of the stomach appeared as a narrow, clear area around the food body, but after a ventrad movement and loss of transparency, only the food body could be seen.

The ventral movement of the stomach was a slow, steady displacement indicating rotation of the entire thorax in the antero-posterior

vertical plane. It is the most important and fundamental development of this period.

In the newly attached cypris the position of the nauplian eye was dorsal and posterior to the paired eyes. During rotation it was displaced, moving ventrad, and then caudad in a rotary manner. Its consecutive positions were found to be accurate indices of the progress of internal development. Soon after attachment, as transparency was lost, the median eye was displaced ventrad until after about forty-five minutes it came so near the sternal surface that in dorsal view it was completely concealed by the body mass. It then moved caudad and came to rest posterior to the compound eyes. The extent to which the whole movement was due to rotation of the thorax was not apparent in observations of living larvae. At its most ventral position the median eye showed a constriction between its halves, present since the nauplius stages. The constriction increased, dividing the eye in half. Division began about two hours after attachment, while still slightly anterior to the brown food body. As it proceeded caudad, and to a point below the stomach, constriction increased. Two and one half hours after attachment the eye was posterior to the food body, and the nearly separate halves appeared diamond-shaped.

The compound eyes prior to this stage consisted each of a central pigmented mass surrounded by a number of clear lenses. Extrusion of the eyes, which takes place at this stage was not visible as a distinct movement in the living organism. Change in position since attachment was evident, however. The pigmented cores migrated about 25 μ antero-ventrally, leaving behind the lenses and associated cells. (Fig. 2). These cores remained within the carapace until the latter was cast off at ecdysis. The lenses, which were at first grouped around the central mass, could not be easily seen in living cyprids, and are discussed more fully later.

No changes were observed either in the highly refractive oil globules present in both anterior and posterior regions, or in the small groups of pigmented granules scattered in the anterior region. Pigmentation in living cyprids was more evident than in prepared specimens in which it was obscured by the opacity of the fixed tissue. The anterior pigment granules were posterior and ventral to the compound eyes; they retained this position in reference to the lenses after the pigmented masses of the eyes had migrated elsewhere. No definite number or arrangement of granules was found. A similar pair of pigmented areas was observed posterior and ventral to the stomach within the sub-

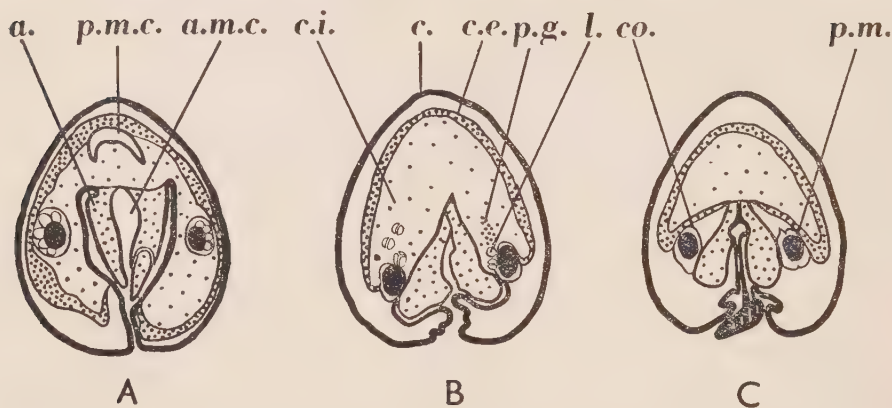


FIGURE 2. Semi-diagrammatic cross sections illustrating loss of compound eyes in *Balanus improvisus* and *B. amphitrite*: (A) cypris during initial attachment, eyes intact; (B) cypris shortly after attachment, lenses being sloughed; (C) cypris prior to ecdysis, section 15 microns anterior to preceding sections. Explanation of abbreviations here and in succeeding figures: *a.*, antenna; *ab.*, abdomen; *add.*, adductor muscle; *a.m.c.*, anterior mantle cavity; *a.n.*, antennal nerve; *b.*, brain or cerebral ganglion; *buc.*, buccal mass; *c.*, carapace; *c.c.*, corneagen cells; *c.e.*, outer layer of corium or mantle folds; *c.e.c.*, circumesophageal connective; *c.f.*, caudal fork; *ch.*, chitin lining mantle cavities or investing thorax; *c.i.*, inner layer of corium; *d.i.*, dorsal invagination; *d.r.*, dorsal retractor muscle; *e.*, esophagus; *e.g.*, esophageal gland; *f.b.*, food body; *h.*, hair-like process; *i.*, intestine; *l.*, lens of compound eye; *l.r.*, lateral retractor muscle; *max.1*, first maxilla; *max.2*, second maxilla; *mn.*, mandible; *mn.p.*, mandibular palp; *n.e.*, nauplian, median or simple eye; *o.*, rudimentary ovary; *o.g.*, oil globule; *p.*, anus; *p.a.*, point of attachment; *p.g.*, pigmented granule; *p.m.*, pigmented mass of compound eye; *p.m.c.*, posterior mantle cavity; *s.*, stomach; *s.e.g.*, subesophageal gland; *s.g.*, shell gland; *st.*, sternite; *t.*, thorax; *t.a.1,6*, first, sixth thoracic appendages; *t.a.e.*, exuvia of thoracic appendages; *t.a.m.*, muscle of thoracic appendage; *U*, U-shaped apodeme; *v.i.*, ventral invagination.

stance of the corium. These were generally obscured in prepared whole mounts.

In contrast to the darkly-colored areas just described were two pairs of light yellow areas, the exact nature of which could not be determined. Especially conspicuous against the transparent surroundings in the earlier period, they remained so until obscured by increasing opacity of the general structure. One pair of these areas was at the most anterior end, and the other was along the ventral edge of the posterior region. They were visible under reflected light when most other structures were indistinguishable, but have not been clearly distinguished in fixed specimens.

Highly refractive oil droplets were among the most conspicuous structures of the living animal, giving a bejewelled appearance to earlier cyprids. They were dissolved during the staining process, leav-

ing large vacuolar spaces. These droplets filled most of the area anterior to the median eye and extended posteriorly along the stomach in two rows. In the posterior region they were located laterally in the corium in two bead-like groups.

About two hours before ecdysis the angle between the longitudinal axis of the cypris and its substrate became marked. It was about 15° . The median eye had divided completely, although the halves remained adjacent for several hours after the molt and appeared to be joined by a connecting pigmented strand. The angle increased until, at the time of ecdysis, the longitudinal axis was perpendicular to the substrate. The parenchymatous anterior disc-shaped areas reached their peak of activity, but few other structures could be distinguished. Viewed end on, the general shape showed a profound change, becoming broader and more flattened ventrally. In the laboratory, ecdysis took place about seven hours after the larva first became firmly attached. The process itself occupied ten minutes from the time that the long axis was perpendicular to the surface and the larva began to kick off the carapace until the time that the molt was complete. Kicking was not continuous, and the cypris would pause for a few seconds after several seconds of activity. A rolling twist of the entire animal accompanied the leg action, and the general appearance was one of violent struggle.

With the region of the adductor muscles acting as a temporary hinge, the carapace was kicked off at the ends, in the manner of a cap being tilted backward (Fig. 3). Before the carapace was cast off, the U-shaped apodemes and attached pigment masses of the compound eyes appeared loosely connected to the carapace by a chitinous ligament, and completely free of the young cirripede. Darwin stated that the carapace split along the dorsal ridge, but evidence from observations here would indicate that the split occurred along the median ventral connection. The carapace was then kicked off by the thoracic appendages. Rotation of the larva within the carapace had reached its limit, so that the halves of the simple eye were beneath the posterior end of the carapace.

In addition to the compound eye-antennal apparatus, ecdysis also included loss of the thoracic exuvium, which remained within the carapace. This would indicate a remaining connection between the thoracic exuvium and the carapace, but none was found. The exuvium of the thorax itself was so delicate that it could barely be seen, but that of the appendages was conspicuous.

The cirri began to beat vigorously in the characteristic adult fashion

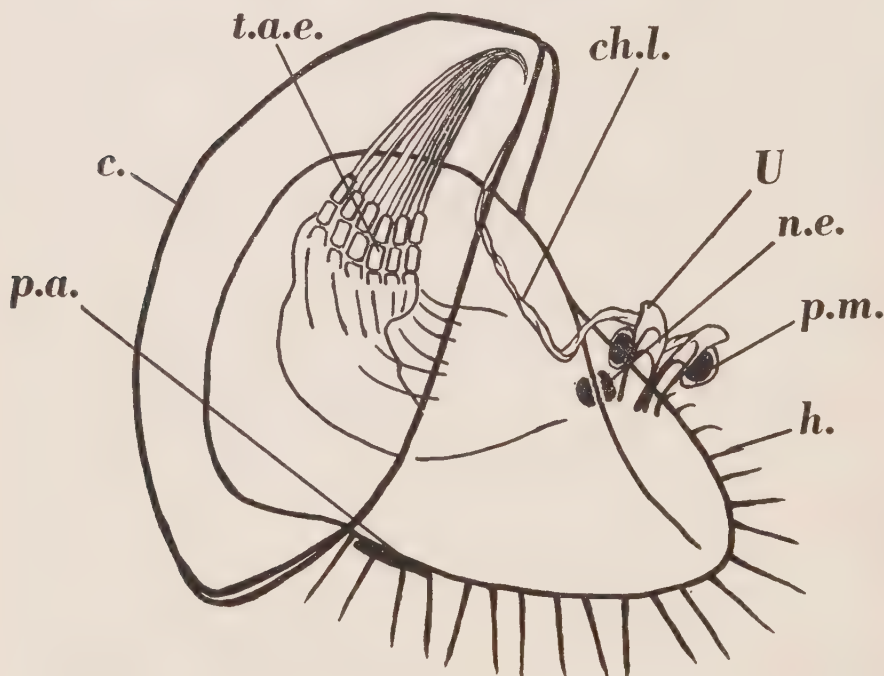


FIGURE 3. *Balanus* during ecdysis, lateral view.

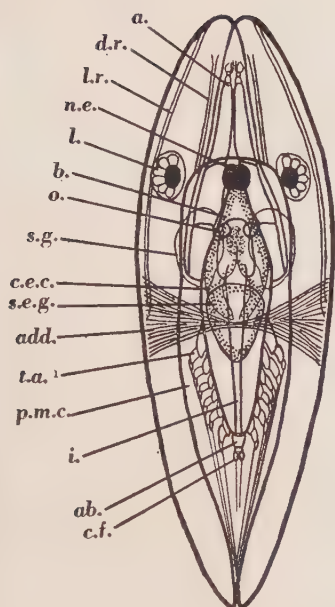
immediately after loss of the carapace. The rolling motion, begun prior to ecdysis, continued and the point of attachment remained small. Rolling was still in evidence twelve hours later, but at a decreased rate of less than once per minute. At this time observations were terminated.

STUDY OF SECTIONED MATERIAL

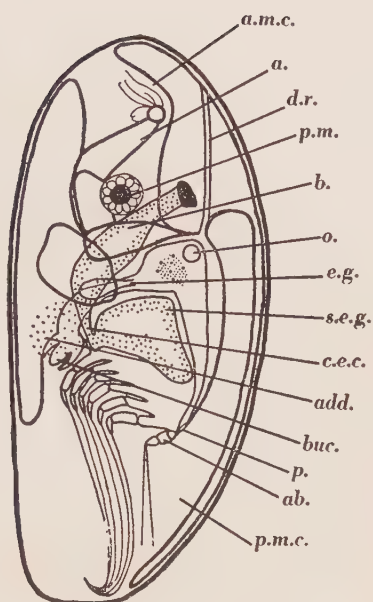
All three body regions of the Crustacea are represented in the cypris. The head accounts for most of the general mass, and the thorax for nearly all of the remainder. The abdomen, vestigial in the adult, is here composed of three small segments and a caudal fork. (*c.f.*, Fig. 4A).

The head may be subdivided into two distinct parts. The pre-oral region occupied about half of the entire organism, and its large size

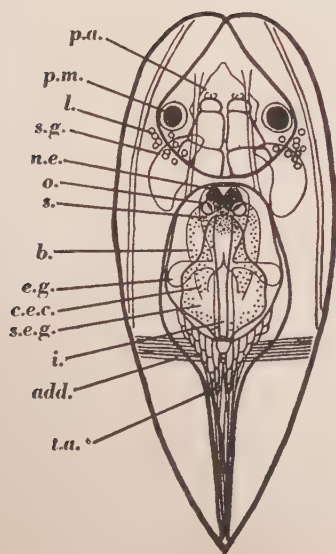
FIGURE 4. Reconstructions of cyprids of *Balanus* sp. During initial attachment in (A) dorsal view and (B) lateral view. Following displacement of internal organs, (C) dorsal view, and (D) lateral view.



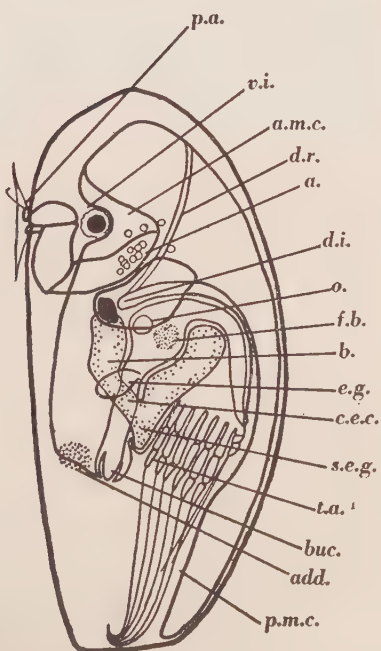
A



B



C



D

was a characteristic feature of this stage. It extended from the anterior end of the animal to the dorsal invagination (*d.i.*) of the posterior mantle cavity, to be described later. Within the pre-oral region, opening on its ventral surface, was a space (the anterior mantle cavity, *a.m.c.*), which accommodated the large retractile antennae. Enclosing this cavity, the corium, or outer layers, extended antero-ventrally as two great downgrowths covered by the chitinous carapace. Within these portions of the pre-oral region were the paired compound eyes and shell glands. The unpaired nauplian eye and cerebral ganglion were the most conspicuous structures in the pre-oral region behind the antennae.

The two head regions were narrowly connected ventrally at the middle of the organism. Posterior to this junction, the oral segments included the buccal mass, directed postero-ventrally before rotation (Fig. 4A, B), and posteriorly afterwards (Fig. 4C, D).

The thorax was always dorsal and posterior to the oral region. Before rotation the longitudinal axis of the thorax formed an inverted L. The fore- and mid-gut ran at right angles to the long axis of the animal and the hind gut ran parallel to it. Following rotation the axis was J-shaped. The fore- and mid-gut ran forward parallel to the long axis and the hind-gut curved dorsally and posteriorly.

The aperture of the posterior mantle cavity (*p.m.c.*) was along the ventral surface behind the adductor muscles, and then upward to the dorsal ridge of the carapace. The cavity was formed by two postero-ventrally directed downgrowths of the corium of the oral region, and was completely invested by thin chitin. Before rotation its anterior end lay dorsal to the thorax as a short, forward-directed pocket. In producing rotation of the thorax and ventro-posterior displacement of the simple eye and brain, this pocket became a deep, ventrally directed invagination, dividing the cypris nearly in two transversely. Before rotation the posterior mantle surrounded the thorax laterally, dorsally and posteriorly; afterwards it also surrounded the thorax anteriorly except for the junction between the two head regions.

The antennae were characteristic and highly specialized structures derived from the first pair of antennae, or antennules of the nauplius. The second pair was lost at metamorphosis from the metanauplius. The point of origin of the antennae was on the antennal somite, or posterior part of the pre-oral region. Sections showed them to be widely separated at their bases, and revealed a large nerve (*a.n.*, Fig. 5A) proceeding into the basal segment from the brain.

Within the more distal portion was a pulpy mass which Darwin identified as the cement apparatus (*c.a.*). No duct was discernible. No glandular structure connected with the antennae was found elsewhere, and it is concluded that the gland producing the cement for initial attachment is contained wholly within the antennae.

The buccal apparatus consisted of a small median labrum and larger paired maxillae. The small labrum was ventral, underlying the mouth and directed posteriorly. Opposite to it, the mandibles (*mn.*) with their lateral palps (*mn.p.*), and two pairs of maxillae (*max.*¹ and *max.*²) lay above and behind the mouth.

The exoskeleton is composed of chitin of varying thickness. The carapace (*c.*) envelops the entire body and appendages when the latter are retracted. By definition, it is limited to the heavy, bivalved external covering and the median ventral connection. The chitin lining the mantle cavities and covering the thorax and appendages is a more delicate membrane (*ch.*) continuous with the carapace proper.

On the ventral side the valves of the carapace are connected by a sternite (*st.*) which is continuous with the valves. This structure is concavely infolded, and is concealed by the ventral portion of the carapace, except in cross section. It is characterized by numerous bilaterally symmetrical folds. Some of these were so prominent as clearly to exhibit secondary folds, while details of other ridges were too minute to be sharply discerned even at a magnification of 970x. In larvae which had just attached, the lateral ridges of one valve approximated those of the other; cyprids shortly before ecdysis showed stretching at this point, and the ridges were more widely separated and distinct. It is evident that the intricate sternal development of the carapace was the result of lateral compression on the sternum by action of the adductor muscles during metamorphosis from metanauplius to cypris. It thus provided for expansion which took care of size changes within the carapace prior to ecdysis.

The paired U-shaped apodemes bearing the compound eyes appeared to be dorsal invaginations of the ventral edge of the exoskeleton in the pre-oral region as described by Darwin. Composed of delicate chitin, they were obscured by the surrounding tissue, but with the pigmented masses of the compound eyes these apodemes were a conspicuous part of the exuvium.

The corium is the true skin of the barnacle. It forms the folds which contain the mantle cavities, and is the organ secreting the exoskeleton. The skin of the inner surface of the mantle folds is different from that

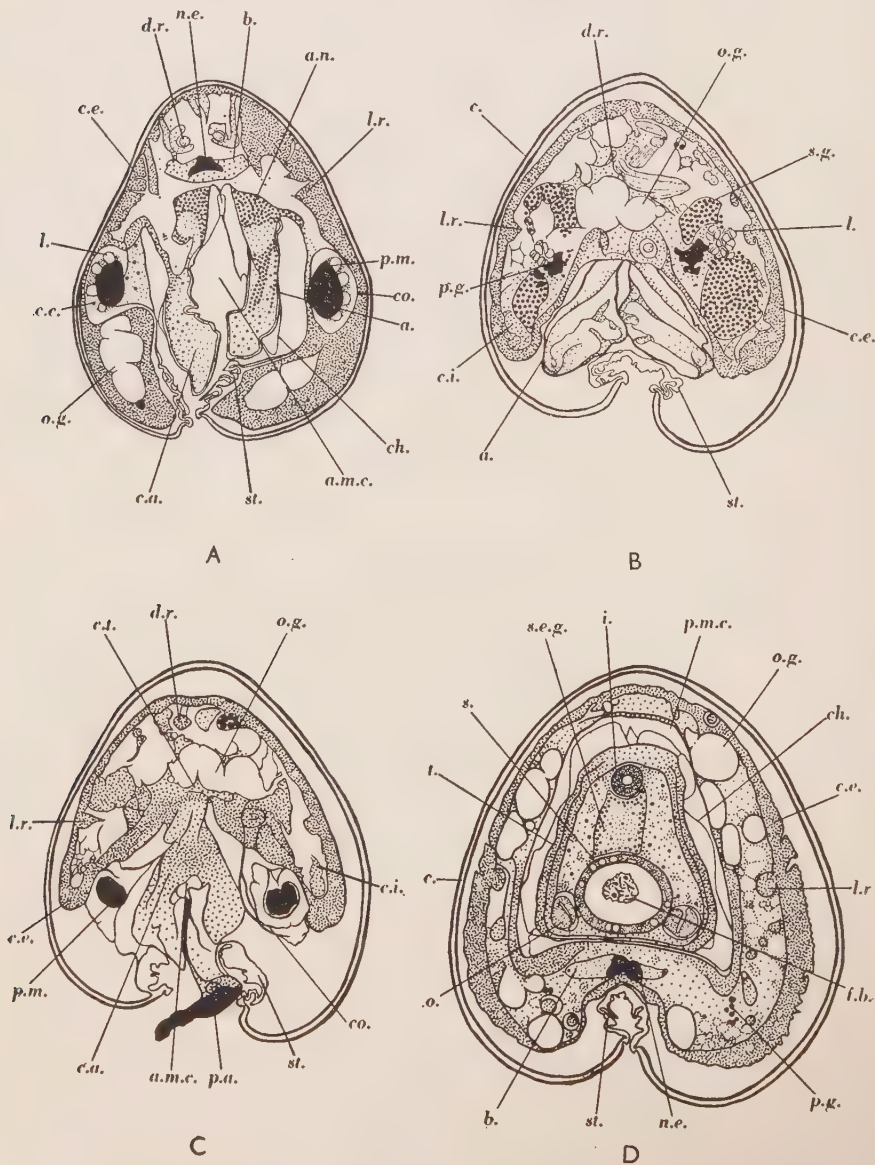


FIGURE 5. (A) Cross section through eyes in cypris of *Balanus* sp. during initial attachment. (B) Cross section through sloughed lenses in *B. amphitrite* just before ecdysis. (C) Section through pigmented masses of compound eyes in *B. amphitrite* prior to ecdysis. (D) Cross section through stomach and nauplian eye shortly before ecdysis.

of the outer; this was especially evident in the posterior region (Fig. 7B). The outer surface of the mantle folds was denser than the inner; its heavy, glandular nature may be correlated with the fact that it secretes the heavier chitin of the carapace. In contrast to this layer was the spongy inner surface which was continuous in the median portion of the pre-oral region with the mesenchymal connective tissue (*c.t.*) in which oil globules (*o.g.*) and anterior nervous and muscular structures were found (Fig. 5A, B).

The greatest concentration of oil was in the anterior head region within the inner layer of the corium (Fig. 5C). Few droplets were present in the outer layer. These droplets may serve a dual purpose. They may be a source of nutriment for the larva, which is believed to take no food at this stage, and they may also provide greater buoyancy for a planktonic existence.

The shell glands were a pair of large, well-defined structures within the substance of the corium of the head (*s.g.*, Figs. 1, 5B, 6A). No ducts were discovered, but their glandular nature was evident.

The general musculature consists of the retractors, the adductors and the appendicular muscles. The dorsal retractors (*d.r.*) extended within the pre-oral region, originating on the dorsal part of the anterior end and inserting on the antero-dorsal part of the thorax over the median eye. The dorsal invagination, the apex of which was immediately above the point of insertion, displaced the latter ventrally, but the muscles remained intact, and might still be traced to the same origin. These muscles produced the previously described cephalad pull on the thorax (Figs. 4, 5).

The lateral retractors (*l.r.*) were a pair of heavy strands which ran along and attached to the inner side of the outer corial layer. They originated at the anterior end of the cypris more ventrally than the previous pair of muscles, and extended caudally as far as the bases of the natatory appendages. They drew the posterior region of the corium cephalad as the dorsal retractors relaxed. As in the latter muscles, there were no opposing muscles; relaxation of the retractors allowed a return of the retracted parts to their original positions. In the adult the lateral retractors are probably concerned with the action of the opercular plates, the rudiments of which they insert upon here. In earlier cyprids these muscles were difficult to distinguish from the outer layer of the mantle fold; they were, however, sharply distinct from the corium in the latter stages.

The most conspicuous and characteristic muscles were the great

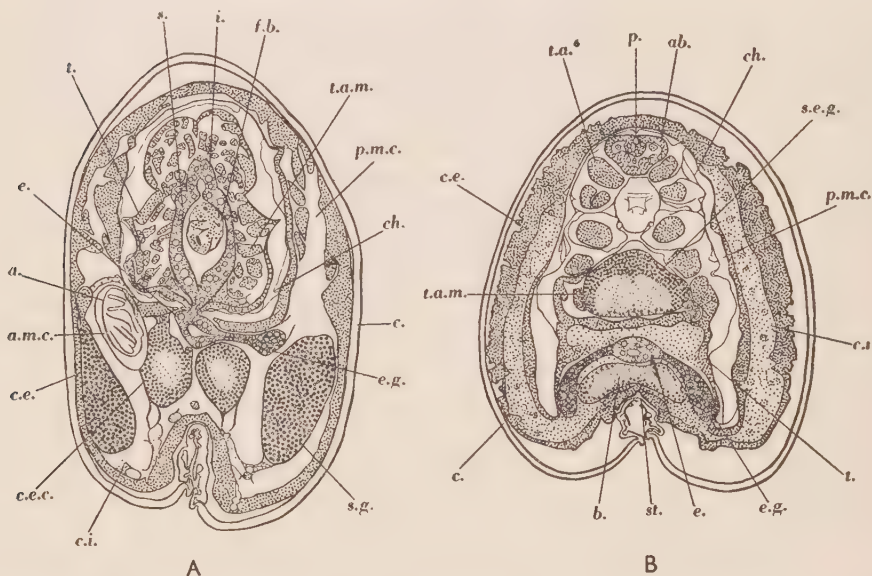


FIGURE 6. (A) Cross section through stomach in *Balanus* sp. during attachment; distortion by lateral compression during sectioning; left half of section slightly anterior to right half. (B) Cross sections through esophageal glands and anus in *B. amphitrite* just before ecdysis.

adductors (*add.*, Fig. 7), visible even in the living animals. They were located in the oral region and extended from one side of the corium to the other, marking the point at which the latter divided ventrally to form the two rudiments of the opercular plates. The two lateral cones of muscle were joined at the median line by a continuous, dense, narrow group of strands, and inserted upon a very thin area of the outer corium. In the early attached larva each half appeared fan-shaped in cross sections, and the median connection lay between the esophagus and subesophageal ganglion in the region of the circumesophageal connectives. During rotation of the thorax the muscles contracted strongly, undergoing change in size, shape and position. The area of insertion on the corium was reduced to one-fourth original size, and the median connection expanded to nearly equal the diameter of the area of insertion, resulting in a shape that was nearly terete. Left behind by the forward and downward swing of the thorax during rotation, the adductors were in the same relation to the corium as previously described, but ventral to the mouth parts and posterior to the subesophageal ganglion. In cross-sections they were stretched

across the posterior end of the sternum, and the areas of insertion were ventral to the median connection. They persist in the adult as adductors closing the scuta.

No dissections were made to determine the exact number of muscles connected with the antennae and apodemes. In sectioned material the position of these muscles was too variable and complex for identification.

The thoracic appendages were well-equipped with muscles (*t.a.m.*, Fig. 7A) originating anteriorly in the thorax. Smaller, but equally distinct, were the muscles of the abdomen (Fig. 6B) and caudal fork.

The digestive system consisted of esophagus, paired esophageal glands, stomach and intestine. The esophagus (*e.*) was a thick-walled tube with a very small lumen, supporting Darwin's statement that the digestive tract here is functionless. In the early attached larva it proceeded cephalad parallel with the long axis for about 25μ and then turned at an angle of about 60° , proceeding dorsally to the stomach (*s.*), which at this time lay in the anterior part of the thorax (Fig. 4B). After rotation, the mouth was shifted caudad and the esophagus was nearly parallel to the long axis (Fig. 4D).

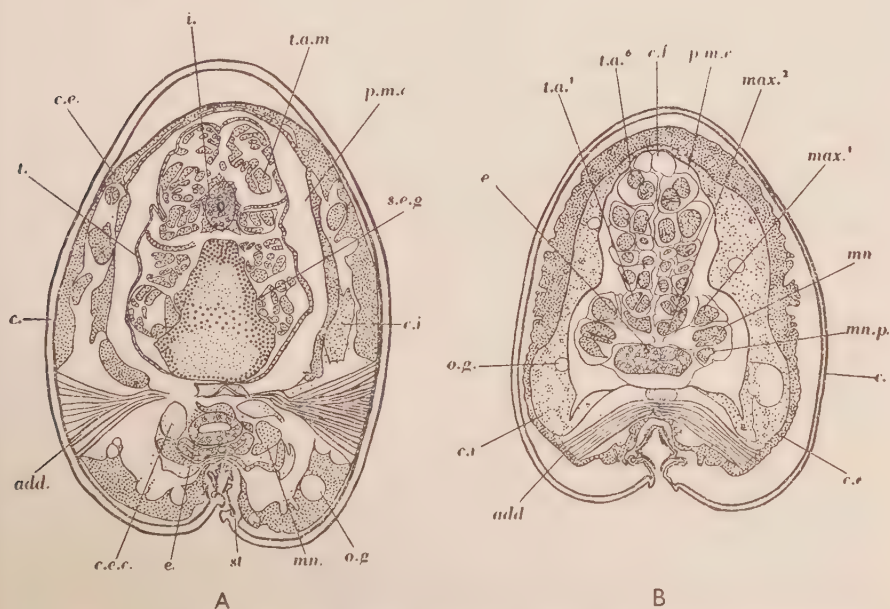


FIGURE 7. Cross section through adductor muscles in *Balanus* sp. immediately after attachment. (B) Cross section through adductor muscles in *B. amphitrite* just before ecdysis.

A pair of pyriform structures connected with the esophagus before the latter joined the stomach. They appeared glandular in nature and are referred to here as esophageal glands. A very narrow lumen extended into them, but the walls were very heavy and the cells filled with a great deal of secreted matter. Rotation of the thorax produced no notable change in them.

After rotation, the stomach lay ventrally in the thorax directly above the simple eye (Fig. 5D). The stomach wall was the thinnest of the entire gut, and the large lumen invariably contained an amorphous food body (*f.b.*) of varying size. The nature of this body could not be determined.

The intestine (*i.*, Fig. 7A) was a simple, thick-walled tube slightly longer than the esophagus. It terminated at the anus (*a.*) between the bases of the caudal appendages (Fig. 6B). Before rotation it lay parallel to the long axis, running in a straight course just beneath the dorsum of the thorax. After rotation, the anterior half of the intestine was pulled ventrally with the stomach, forming a curve with the posterior half which still lay dorsally, but more anteriorly than before.

The gonads appear in the cypris as incipient ovaries; there is no indication of the testes. In the more primitive Branchiopoda (*e.g.*, *Apus*) the ovaries are thick-walled, hollow structures on either side of the gut. Similar paired structures (*o.*, Fig. 5D) with thick walls and a very small lumen were found in the thorax adjacent to the stomach as very short tubes, but exhibited no definite connection with the stomach or any of the other organs. In one instance, however, a longitudinal section revealed a duct passing posteriorly from one of these bodies, traceable to the region of the bases of the thoracic appendages. The Cirripedia are characterized by location of the female genital opening at the base of the first pair of thoracic appendages in the adult. Before rotation these bodies were adjacent and lateral to the antero-dorsal portion of the stomach; afterwards they could be seen ventral to their original position, still in contact with the same region of the stomach, displacement of which has been described above. Their structure and position suggest homology with Branchiopod ovaries, and their position in the cypris was near that in the adult, in which they are later supposed to migrate into the base.

The nervous system as observed here was composed of three eyes, two large ganglia joined by a pair of circumesophageal connectives, and the antennal nerves.

The displacement of the simple eye was mentioned before, but

explanation of it was dependent on study of sectioned material. With increase of the dorsal invagination ventrally, the eye was drawn sharply downward and backward to a position below the simultaneously displaced stomach. No nerve connection between the eye and cerebral ganglion (*b.*) could be found due to their closeness to each other.

The more complex paired eyes are present in two larval stages, metanauplius and cypris. Surrounding a pigmented core (*p.c.*) on every side except medially are ten to twelve lenses (*l.*), and enclosing the combined structures is a thin cornea (*c.*). The lenses were conspicuous in stained sections as bright blue, clear spheroids. No explanation for their peculiar staining properties has been found. A small amount of tissue at the bases of the lenses were identified as corneagen cells (*c.c.*), which are considered to secrete the lenses.

Shortly after attachment the corium surrounding the eyes began to be resorbed. Accompanying this change was the ventral invagination of the pre-oral region, produced as a transverse fold within each side of the anterior mantle folds. The lenses and corneagen cells were sloughed away from the central core and migrated posteriorly where they came into contact with the shell gland (Fig. 5B) or were scattered throughout the pre-oral region by the periodic convulsions of the organism at this time. Pigmented cores and corneas were forced downward and outward by the receding corium. Thus they were extruded from the corium while still within the carapace. Loss of these organs during ecdysis has already been described.

The cerebral ganglion, or brain, was a prominent structure directly behind the median eye. Before its displacement by the dorsal invagination, it lay obliquely as viewed from the side. At its antero-dorsal end it was in contact with the nauplian eye, while postero-ventrally in the region of the esophagus, it split to form circumesophageal connectives (*c.e.c.*) which joined the subesophageal ganglion (*s.e.g.*). Slightly below the median eye large antennal nerves (*a.n.*) were found in sections of earlier cyprids. With degeneration of tissues associated with the antennae, the antennal nerves were similarly lost, and had no further significance.

The subesophageal ganglion was the largest nervous structure. It is homologous with the subesophageal ganglion and ventral nerve cord in other Crustacea, and not merely with the thoracic ganglia alone. In neither sagittal nor cross sections did it appear as a chain, but as a massive, bent bar lying posterior and ventral to the three regions of

the gut. Numerous small nerves from this ganglion supplied the buccal apparatus and thoracic appendages, but they were lost in the surrounding tissue before they could be traced to their termini.

The appearance of these ganglia and nerves in section was typically divided into an outer, heavily stained nucleate region, and an inner, lightly stained enucleate region.

Neither the respiratory nor circulatory system has been described as such in the Cirripedia for any stage. In the Ostracoda, where definite branchial structures are absent, gas exchange occurs across the inner lamella of the shell and the whole surface of the body (Sedgwick, 1909). The chitinous lining (*ch.*) of the mantle cavities of the cypris was exceedingly thin, and this lends credence to the probability that these cavities perform the functions of respiration.

A heart or any other definite vascular structures are notably absent in the entire subclass.

DISCUSSION

The attachment process and the previous period of creeping have been described by Visscher (1928b). Few references were found regarding the changes occurring within the cypris during the hours intervening between attachment and ecdysis, however, and they have therefore been described in detail here.

Numerous authors have described the more general features of ecdysis. Burmeister (1834) was the first to record that the eyes and supporting apodemes were cast off with the carapace, and has been supported in this view by Darwin (1851), Hesse (1874), Visscher (1928a) and Herz (1933). Von Willemoes-Suhm (1876) and Fales (1928) contended, however, that the eyes lost their original position and were resorbed in the adult as pigment spots. Loss of the eyes in *B. amphitrite* was found by Visscher, and Fales confirmed it after study of his slides.

It is difficult to believe that such a wide variation in a fundamental process exists within a single genus. Pigment spots such as those described by Von Willemoes-Suhm and Fales were clearly observed to be separate, independent bodies before any change took place in position or structure of the eyes. They did not undergo any noticeable alteration during the breakdown and extrusion of the eyes. The lenses remained in the young cirripede apparently unchanged five days after the molt; but in all cases observed, the central pigment masses were invariably extruded as such.

The observed molting of the carapace simultaneously with the exuvia of the thorax and thoracic appendages is contrary to the observations of Darwin (1854). He stated that the thoracic exuvia were cast off considerably later than the carapace.

Darwin referred to the posterior mantle cavity simply as the mantle cavity. Although he and other investigators recognized that the antennae could be withdrawn into the carapace, the cavity into which they were withdrawn was not specifically described. It is now proposed that the names anterior mantle cavity and posterior mantle cavity be used to distinguish them. No physical connection existed between them. They are both, however, of the same nature, and are contained by flap-like outgrowths of the corium of the dorsal head region directed both forwards and backwards.

The earliest workers (Burmeister, 1834; Bate, 1851) assumed that the valves were, as in the ostracods, free at their ventral edges, held together only by the large adductor muscle. Darwin figured a ventral plate (1854, Pl. XXX), but showed it as independent of the carapace. Claus (1869) stated that the valves hung together firmly on the ventral edge, and mentioned a connecting seam. The sternite, however, shows clearly in sections, and is entirely different in character than the plate of Darwin or seam of Claus. The probable value to the cypris of the sternal folds is to allow expansion during metamorphosis. It is evident that the intricate sternal development was the result of lateral compression on the sternum by action of the adductor muscles during metamorphosis from the metanauplius. It thus provided for expansion and allowed size changes within the carapace before ecdysis.

No dissections were made of the antennae; they have been carefully dissected by Claus (1869), and little was found to add to his description of their structure or musculature, both of which are highly organized. He stated that the antennal bases in *Lepas* were fused. Sections showed them to be widely separated in the species studied here, as described by Darwin for the Balanidae.

The shell glands are obviously identical with the reniform glands described by Groom (1895a), who offered no suggestion as to their function. Neither Burmeister, Darwin, Claus nor Hoek (1884) found comparable structures in *Lepas*. Herz identified the shell glands in *Balanus crenatus*, and reported small ducts passing dorsally from them. He was unable to trace the ducts to their ends.

In the Branchiopoda, from which the Cirripedia are considered to

have been derived, there are paired shell glands in the head region. They are nephridial in function and structure, and have been referred to as renal organs and maxillary glands. They have been described in adult barnacles, and are the characteristic excretory organs of lower Crustacea. No postulate as to the function of these glands in the cypris is made here, but their position and glandular structure may be evidence of homology with the shell glands of the Branchiopoda.

The dorsal retractors were previously described by Herz, but the lateral retractors are here described for the first time. They are not apparent in any view other than cross section. The adductors and muscles of the thoracic appendages have been described by all previous investigators.

The esophageal glands were identified by Darwin as caeca connected with the stomach. Later investigation by Claus, Hoek, and Coker (1901) demonstrated their connection with the esophagus. No agreement, however, was reached in regard to their function. Darwin, Hoek and Coker referred to them as caeca. Claus named them Leberhörnchen, assuming a glandular function. In view of their position and glandular nature, as seen in sections, they are referred to here as esophageal glands.

Darwin and Hoek described paired incipient ovaries in the cypris of *Lepas*. Both found them as elongate structures whose duct opened immediately antero-dorsally to the adductor muscles during the post-rotational period. The anterior portion of these glands extended into the pre-oral region, traversing the narrow ventral connection with the oral region. Darwin stated that the incipient ovaries were derived from the gut-formed cement glands. Claus noted a duct connecting with three small diverticula far posteriorly into the mantle in a similar position to the ovarian tube in the ostracod *Cypris*. It was much farther posteriorly than the cement gland ovaries of Darwin, and Claus therefore considered it highly improbable that they were homologous. The organs here identified as incipient ovaries are not identical with those of any previous workers. Their resemblance in position and structure to the ovaries in the more primitive Branchiopoda is marked, however.

SUMMARY

1. Larval stages of *Balanus improvisus* Darwin and *B. amphitrite niveus* Darwin were studied from time of attachment to metamorphosis to the adult. Particular attention was paid to features of internal anatomy by means of microsections.

2. Cyprids of the two species were distinguished and the differences described and figured.

3. Approximately seven hours elapsed between initial attachment and ecdysis.

4. During ecdysis the exuvia of the thorax and thoracic appendages are cast off in addition to the carapace, apodemes and compound eyes.

5. The changes in the position of the internal organs which have not hitherto been clearly explained are described and figured. Two basic changes occur during this period. Most important is a rotation of the thorax and oral region of the head in the antero-posterior vertical plane, and a postero-ventral displacement of the median eye and cerebral ganglion. This is caused by a dorsal invagination which divides the larva almost in half between the pre-oral and oral regions of the head. The second change involves extrusion of the pigmented masses of the compound eyes and adjacent apodemes at ecdysis, and is effected by a ventral invagination into the corium from the pre-oral region.

6. No differences in internal anatomy of the two species studied were apparent.

7. A description is given of the intricate folds of the sternal portion of the carapace. The sternum is shown to unite the valves, with which it is continuous.

8. The fate of the nauplian eye and of all parts of the compound eyes in these species is fully described. Previous accounts of this have been both incomplete and conflicting.

9. The paired shell glands are described and their homologies with the maxillary glands of other Entomostraca are discussed. No distinct cement glands were found other than those of the antennae.

10. Paired lateral retractor muscles are described.

11. Previous accounts of the digestive system and buccal structures are generally confirmed by detailed observations on the species studied.

12. Paired rudimentary ovaries and an incomplete oviduct in the thorax are described. The position and relations of these organs do not agree with descriptions given by previous authors.

13. The central ganglia of the nervous systems are described and figured. There has heretofore been no complete account of these.

14. Gas exchange apparently occurs across the thin chitin of the mantle cavities. There is no well-organized circulatory system.

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The Species of Oysters of the Gulf, Caribbean and West Indian Region

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THE GENERA OF OSTREIDAE

Pycnodonte

THE TRUE OYSTERS, family Ostreidae, have three living genera, all of which occur in this area. The least common is *Pycnodonte* Fischer de Waldheim 1807. Very little is known about the natural history of this group. The species are of no commercial importance and live at depths from 10 to 1,000 fathoms. They are differentiated from all other ostreids by the fact that the intestine passes through the heart and they have a peculiar cellular structure of the shell unlike that of any other mollusk. Fossil *Pycnodontes* are very easily distinguished by this characteristic. These oysters are known to go back for 60,000,000 years to the upper Cretaceous period in geological history. The *Pycnodontes* are also distinguished by characteristics of the prodissoconch shell. Only one living species is known to exist in the Gulf and Caribbean region. It was described as *Ostrea thomasi* by MacLean in 1941. It came from 50 fathoms of water in the Atlantic Ocean off Palm Beach. It is evidently a *Pycnodonte*, as shown by the cellular structure of the shell.

Ostrea

A second genus is *Ostrea* of Linnaeus 1758. The type is *O. edulis*, the oyster of northern Europe, which made gastronomic history long before America was discovered. Oysters of this group are relatively flat and round. Often they are wider than long. The adductor muscle is situated almost in the middle of the shell. The muscle scar is unpigmented. In contrast to the following genus they are smaller and have thinner shells and most species have teeth or denticles on the inner valve margins. They have only one exhalent outlet. Oysters of this group produce relatively large eggs which are held within the gills and mantle chamber until the larvae are in an advanced stage of development. For that reason they are called larviparous. They live in waters of relatively high salinity (25 to 35 *per mille*) and are not found far inside estuarine waters. Examples of this genus are scattered

all over the world except in very high latitudes. Oysters are known from all continents except Antarctica.

There are four species of *Ostrea* in North America. The best known are *O. lurida* of the Pacific and *O. equestris* Say of our south Atlantic and Gulf coasts. On the northern Gulf coast this little oyster is not commonly seen, although it has been reported to be numerous at times around Apalachicola. It has been observed in Louisiana and far down the Texas coast, within 100 miles of Mexico. It is sometimes found in the bays when the salinities are high and has been found living on hermit crab shells 5 miles out in the Gulf of Mexico (Gunter, 1950b). Recently the writer found large specimens, up to 72 mm. in length, growing on oil well platforms off the Texas coast. They grow to that length in a year's time. Similarly, large specimens have been found on oil well platforms off the Louisiana coast. These oysters have a brittle shell and large areas of the periostracum have cracked off in a relatively short time. They have well-formed teeth on each side of the hinge in the upper shell which fits into depressions of the lower shell. These teeth may be present in a short ridge only a centimeter or so in length or they may extend almost around the total circumference of the shell. The edges of the valve of *O. equestris* may be perfectly smooth but in some specimens the lower shell is finely zigzag or coxcombed where it meets the upper shell. Nevertheless, the upper shell fits on the inside and is usually not zigzag. Oysters of this genus do not form large reefs and are not as prolific as our common American oyster, even in Europe where they are cultivated. The few *O. equestris* on the Gulf Coast which are of adequate size for eating have an excellent flavor. These oysters are of great theoretical and biological interest for several reasons but they will never be of commercial importance in our region. It has recently been found by Dr. S. H. Hopkins that they are hosts to *Nematopsis*, the common oyster parasite discovered through the keen observations of Dr. H. F. Prytherch.

Fischer de Waldheim in 1807 set up the genus *Alectryonia* for the tree oyster. They were again designated as *Dendostrea* by Swainson in 1835. These oysters do not have a promyal chamber. The muscle scar is unpigmented, and so far as is known they are larviparous. Here we might mention the very fine contributions of Dr. Gilbert Ranson of the Muséum National d'Histoire Naturelle of Paris, who has shown that characteristics of the prodissoconch shell of the tree oyster are the same as those of *Ostrea* and different from *Crassostrea* and *Pycnodonte* which are also separable from each other. Therefore, in spite of the many genera which have been described, Ranson reduces them to three

and places *Alectryonia* and its synonym *Dendostrea* with *Ostrea*. To the writer that seems to be a reasonable judgment. The only remaining characteristic by which the tree oysters are separated from *Ostrea* is the fact that they can produce extensions or hooks of the lower valve which curl around and sometimes interlock over Gorgonia stems and mangrove roots. However, Woodring (1925) has pointed out that the tree oyster does not necessarily have these hooks when growing on flat surfaces.

The tree oyster of the West Indies is usually described under the name of *Ostrea frons* (Linnaeus). Lamarck called some of them *O. limacella*. Examples obtained from the U. S. National Museum show that *O. limacella* is a long, slim oyster with thick heavy interlocking margins of the two valves on each side and with hooks around the stems of organisms on which they grow. It seems that this so-called species is only a variant of *O. frons*.

In February, 1950, the writer discovered the tree oyster living on oil well platforms 5 miles offshore on the Louisiana coast. They were longer than wide and grew attached by the flattened surfaces of the lower valves to the templates of the oil well platforms. Obviously they could not extend hooks around these large structures, which are some 8 to 10 inches in diameter, but there were small remnants of hooks near the hinge and along the right margin. These oysters were of excellent flavor. This is the first record of the tree oyster from the northern Gulf of Mexico. It is known to grow along the mangrove roots of south tropical Florida and is said to extend as far north as the coast of North Carolina. It is sometimes known as the coon oyster and therefore various workers have confused it with the long, slim *O. virginica* which is also known as the coon oyster. For that reason it has been previously reported from the bays of the Texas Coast. However, none live there and, so far as the writer knows, none live in waters of low salinity. Similar to *O. equestris*, the tree oyster has teeth but they are very irregular and unlike the precise dentition of *O. equestris*. In addition, various patches of tuberculations are found on both upper and lower shells. A little examination enables one to tell rather quickly the difference between the marginal dentition and tuberculations of the two species.

There is a small oyster living among the bread sponge in shallow waters of the coast of Florida and the West Indies which has a non-pigmented muscle scar and teeth along the margin of the valves. The shell is smooth and the beaks are strongly curved. It is called *Ostrea permollis*.

Crassostrea

The third genus of living oysters is properly called *Crassostrea* of Sacco in 1897. Orton and various French workers have long recognized that this genus was separate from *Ostrea* of Linnaeus. It is characterized by the fact that it is longer and larger, has a thicker shell, lives in waters of a lower salinity, casts the eggs and sperm directly into the water and may lay up to 50 million eggs at a time. It has a second exhalant stream which comes out in front of the muscle and is therefore known as the promyal chamber. The muscle scar is usually pigmented. T. C. Nelson maintains that this chamber is an adaptation to the more estuarine and more turbid waters in which species of this genus live. The species have the capacity of forming huge reefs. In Texas and Louisiana buried reefs of the common American oyster are the foundation for a huge industry of mudshell dredging. Several million cubic yards are dredged along the northern Gulf Coast each year.

French workers and some Americans have designated this genus *Gryphaea* on the supposed grounds that it was described by Lamarck and that the type species is *G. angulata*, the Portuguese oyster. However, Lamarck did not describe the species, but in his original work said he would do so later. Even under the somewhat lax rules which applied in the older times, Lamarck's statement could not be considered a valid description. Some workers have held that, since *G. angulata* was later validly described by Lamarck and subsequent workers, that it is the valid type of the genus. However, the rules of the International Commission for Zoological Nomenclature definitely state that an originally undescribed species is a *nomen nudum* and is not available as a generic type in any later publication. The case is further complicated by the fact that Lamarck did describe properly certain fossil species under the name *Gryphaea*. One of these, *Grphyaea arcuata*, was selected as the type of a fossil genus by Anton in 1839. It is quite a different genus from the modern oyster and became extinct some 60,000,000 years ago. This is the group called *Liogryphaea* by some paleontologists.

In 1897 Sacco, an Italian who apparently worked at conchology as a hobby, set up the genus *Crassostrea* with *C. virginica* as a type species. Sacco contributed very little to oyster biology and published in obscure journals. It so happened that he was the first man legitimately to designate this genus. *Crassostrea* means thick-shelled and apparently Sacco realized that this genus had never been properly designated. The name is not particularly euphonious and the writer must admit that in his own efforts to work out the situation he tried

hard to validate another genus, but it would not hold. Therefore, the only possible proper name of our American oyster is *Crassostrea virginica* (Gmelin). These facts have been previously reviewed in more detail (Gunter, 1950a). Other members of this group are the Portuguese oyster, *C. angulata* (Lamarck) and *C. gigas* (Thunberg) of Japan. There are many others. This genus is also distributed over most of the tropic and warm temperate world. The common American oyster, *C. virginica*, is doubtless the most prolific species on the face of the earth. There was a time when Chesapeake Bay produced more oysters than all the rest of the world, and the Louisiana Coast does not fall far behind. Along the Mexican coast, about 200,000 gallons of these oysters are produced annually.

There is a second well-known species of this genus living in Cuba called *C. rhizophorae*. It seems to have a muscle scar less heavily pigmented than is usual with the genus. Mattox (1949) has reported that no evidences of alternational hermaphroditism have been found in the species. If this is the true case, it is the only oyster of the above two genera, which have been examined, showing a lack of alternational hermaphroditism. This species is of some commercial importance in Cuba and the West Indies. It seems to live in waters of somewhat higher salinities than other known members of the genus. It is differentiated from *C. virginica* by various characteristics of shell, one being the fact that the upper or right valve is uniformly depressed or set within the lower valve. There is a similar or cognate species living along the coast of Baja California, Mexico. So far as is known, it has never been described and the writer has seen only a few examples.

OYSTERS OF LOUISIANA

The common estuarine oyster, *C. virginica*, the "horse" oyster, *O. equestris*, and the tree oyster, *O. frons*, were all found living together on oil well platforms off the Louisiana coast, the common oyster living at higher levels and the other two at overlapping but lower levels. It has recently been shown by Geyer (1950) that the waters of the Louisiana coast out to 5 and 6 miles offshore undergo seasonal variations of salinity ranging from 15 to 35 parts per thousand at depths of 10 feet. This explains why the estuarine oyster, *C. virginica*, is found at such distances from shore in the open ocean. The common oyster is also found at about the same distance from land on oil well platforms off the Brazos River of the Texas Coast. The tree oyster has not been heretofore reported from Louisiana and one wonders where the larvae came from. They could hardly be expected to have followed currents

around the Gulf, as Walton Smith postulated for the spores of the sponge disease. Most probably tree oysters have been present throughout modern times around the coral heads in the offshore waters of the northern Gulf.

SUMMARY

There are species of all three living genera of Ostreidae in the Gulf and West Indian region. They are *Pycnodonte thomasi*, *Ostrea equestris*, *O. frons*, *O. permollis*, *Crassostrea virginica*, and *C. rhizophorae*. Table I lists the species and their known distribution. *O. limacella* seems to be a synonym of *frons*. *O. sprete* is in part a synonym of *equestris*.

TABLE I. OYSTERS OF THE GULF-CARIBBEAN REGION

<i>Pycnodonte</i>	OSTREIDAE <i>Ostrea</i>	<i>Crassostrea</i>
<i>P. thomasi</i> (McLean) (S.E. Florida)	<i>O. equestris</i> Say (South Atlantic, Gulf Coast, and West Indies.)	<i>C. virginica</i> (Gmelin) (Atlantic and Gulf Coasts to Mexico and Brazil)
	<i>O. frons</i> (Linnaeus) (West Indies, South Florida, Louisian)	<i>C. rhizophorae</i> (Guilding) (Cuba, Puerto Rico)
	<i>O. permollis</i> Sowerby (Florida and West Indies)	

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Marine Borer Attack in Relation to Conditions of Illumination¹

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ILLUMINATION as a factor influencing the attachment of sessile marine organisms has received considerable attention during recent years, largely because of its relation to the economically important problem of ship bottom fouling. Possibly for the same reason, investigations have been mainly directed towards the immediate gross effect of varying conditions of illumination, rather than towards an analysis of the fundamental nature of the behaviour of the organisms involved.

Experiments carried out upon various species of barnacles by a number of investigators have been summarized by Smith (1948). They show that, in daylight, darker colored or shaded surfaces are more rapidly colonized by barnacles but that during the hours of darkness the intensity of attachment is greatly reduced. Surfaces weakly illuminated by artificial light during the night time, however, are settled as rapidly as the dark surfaces during daylight hours, according to Weiss (1947).

Visscher (1928) and others subjected barnacle larvae to experiments under laboratory conditions and showed that these organisms swim away from the lighted side of a vessel. This in itself does not explain all of the gross phenomena previously referred to. Smith (1948), however, describes the distribution of larvae over black and white squares of various sizes, on the basis of which he concludes that the maximum amount of attachment occurs in a low optimum intensity of diffuse light. He suggests that this effect is due to a tendency on the part of the organisms under the influence of optimum light conditions to remain upon whatever surface they chance to encounter rather than to a phototropotaxis. Unfortunately this hypothesis was not subjected to experimental analysis using larvae under controlled laboratory conditions.

The comparative lack of detailed analytical study of the behaviour

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of marine invertebrate larvae undoubtedly arises from difficulties encountered in maintaining sufficiently large numbers of larvae under laboratory conditions. One of the most detailed investigations is that of Lynch (1947) who was able to secure and maintain healthy larvae of *Bugula neritina* under experimental conditions. In this and subsequent investigations (Lynch, 1949) he was able to show the effects of varying salinity, temperature and other conditions upon response to gravity and light. He does not, however, distinguish clearly between taxes and kineses.

Careful analysis of the behaviour of marine organisms with respect to light conditions has been carried out in the case of planktonic organisms such as the copepods *Centropages typicus* (Welsh, 1933), *Acartia tonsa* (Schallek, 1943) and *Calanus finmarchicus* (Clarke, 1934), and in the case of mysids (Foxon, 1940). The results show different responses to directional and diffuse illumination and suggest that under different conditions either phototropotaxis or photokinesis may be involved.

The effects of light upon marine borer attack have not been studied in detail. Henderson (1924) mentions that Limnoria activity is inhibited by strong light. The relationship between illumination and the boring of teredids does not appear to have been subjected to detailed investigation.

During the course of recent studies upon the biology of shipworms a technique was developed for maintaining large numbers of healthy larvae under laboratory conditions. The opportunity was therefore taken to analyze in detail the light reactions of these larvae in conjunction with studies of borer attack upon panels under conditions of controlled illumination.

In carrying out the experiments assistance was rendered by William S. Shoemaker, who carried out the light measurements and by other members of the Laboratory staff, whose help is gratefully acknowledged.

SUBMERGED PANEL EXPERIMENTS

In the following experiments, various types of panel exposures were examined for borings. The tabular results given do not distinguish between the various species of teredids, since it was found impractical to identify individual burrows. Frequent checks, however, showed that the species *Teredo* (*Lyrodus*) *pedicellata* was conspicuously in

the majority, and usually caused over 95% of the attack. It may therefore be concluded that, for practical purposes, the investigations are based upon this species alone. Attacks by *Bankia fimbriatula* did not occur in sufficient numbers to be of significance in these experiments. The single *Limnoria* species has been identified as *Limnoria lignorum*.

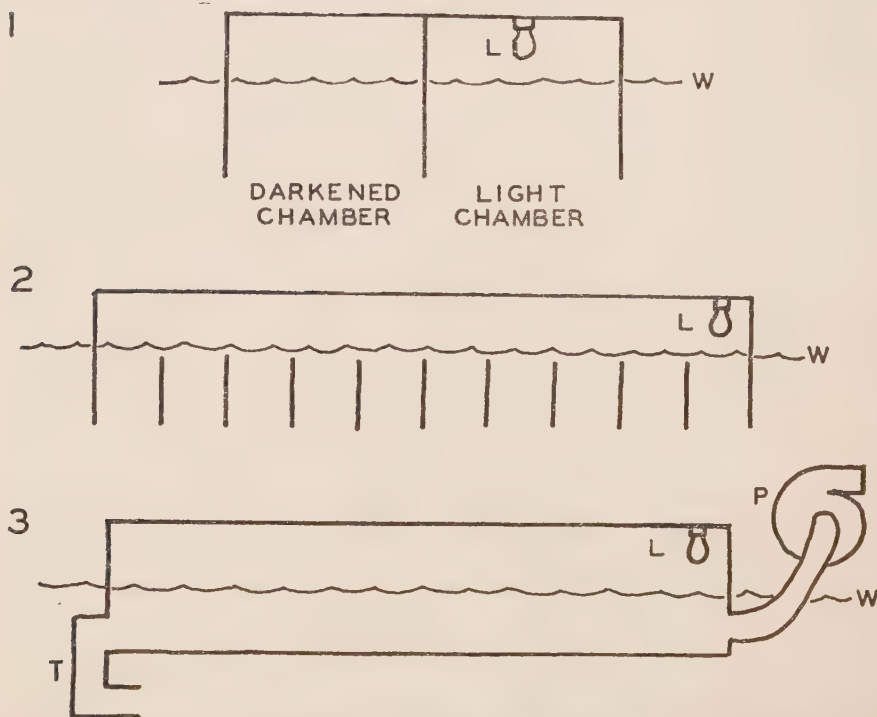


FIGURE 1. Diagram of arrangement for panel tests. (1) First and second experiment. (2) Third experiment. (3) Fourth experiment. W, water level. L, lamp. P, pump. T, light trap at intake end of chamber.

First Experiment. Four separate experiments were carried out in which wooden panels were submerged in and enclosed by a floating box, moored at the Causeway Terminal Yacht Basin, Miami Beach. In the first experiment the panels were contained in two compartments, both of which were open only at the bottom. One compartment was illuminated from above by means of an electric light bulb, whereas the other was not illuminated except for the natural light entering from below. (Fig. 1) The intensity of illumination was measured by means of a photocell placed immediately beneath the open base and directed

upwards. A second reading was taken inside the chamber with the cell directed downwards.

The results (Table I) show that, with a 40 watt bulb the greater number of borings of each organism occurred in the lighted chamber, but that the results were not statistically significant.

Second Experiment. In a second experiment, using the same apparatus with a 150 watt bulb, the illuminated panels experienced a barely significant lesser attack than those in the dark chamber. This was true of both *Teredids* and *Limnoria*. (Table I).

TABLE I
RELATION OF MARINE BORER ATTACK TO INTENSITY
OF ILLUMINATION. PANEL EXPERIMENTS I AND II

COMPARTMENT	ILLUMINATION IN FOOT CANDLES				NUMBER OF BURROWS IN EACH PANEL		
	Day		Night		Teredo	Bankia	Limnoria
	Up*	Down*	Up*	Down*			
I **Unlit	30	13	0	0	50(a)	0	8
**Lit with 40 watt bulb	145	90	30	2	61(a)	2	12
***Unlit	50	12	0	0	40(b)	0	16
II ***Lit with 150 watt bulb	350	97	50	12	24(b)	1	5

* Direction faced by photometer.

** January 23, 1949, to February 22, 1949.

*** April 7, 1949, to May 7, 1949.

(a) Deviation 1.1x standard error for equal distribution.

(b) Deviation 2x standard error.

Third Experiment. An attempt was made, in a third experiment, to examine the effects of intermediate ranges of illumination and to provide results which would be statistically more reliable. For this purpose a long floating box was divided into a series of compartments, open at the bottom and illuminated from a continuous gallery above. The illumination was provided by a lamp at one end of the box, so that the amount of light entering each compartment was successively less from one end of the series to the other. (Fig. 1) The results show a considerable increase in borer attack under conditions of illumination indicated by light readings of 30 to 145 foot candles at the entrance to the compartment, with the photometer cell facing upwards at the lower entrance. Borer attacks dropped very rapidly both above and below this light range. They were most numerous at 37 foot candles by day and 30 foot candles by night. (See Table II) *Limnoria* borings were almost entirely absent.

TABLE II
RELATION OF MARINE BORER ATTACK TO INTENSITY
OF ILLUMINATION. PANEL EXPERIMENT III*

Compartment	ILLUMINATION IN FOOT CANDLES		Average number of teredid burrows in each panel
	Day	Night	
1	500	395	86
2	145	140	144
3	58	40	139
4	37	30	185
5	20	17	50
6	1	2	54
7	0	0	55
8	0	0	62
9	0	0	68
10	0	0	70

* July 18, 1949, to August 18, 1949.

Fourth Experiment. In order to provide a continuous variation in light intensity and in order to exclude the change in intensity of illumination from day to night a completely closed box, six feet long, was constructed. Water was drawn through the submerged apparatus by means of a pump at one end and an opening with a light trap at the opposite end. The interior was painted white and a 150 watt bulb was inserted at one end. Two test panels, six feet long and six inches high ran the length of the box. In this manner a continuous drop in light intensity occurred from one end of the panels to the other. Light readings were taken at one-foot intervals by means of a photocell drawn along the floor of the box.

At the end of the experiment the panels were removed and the number of burrows counted in each one-foot section. (Fig. 2) The results show that the greatest intensity of teredid attack occurred under conditions of illumination represented by a measurement of 50 foot candles with the photocell facing the panel, or 166 foot candles with the instrument facing upwards. At both higher and lower degrees of illumination the intensity of attack was considerably less. In the case of *Limnoria* the boring activity was greatest under the conditions of least illumination.

LABORATORY EXPERIMENTS

General. The young of *Teredo pedicellata* are retained in a modified portion of the maternal gill cavity during the greater part of development and, under normal conditions, are free-swimming for a period

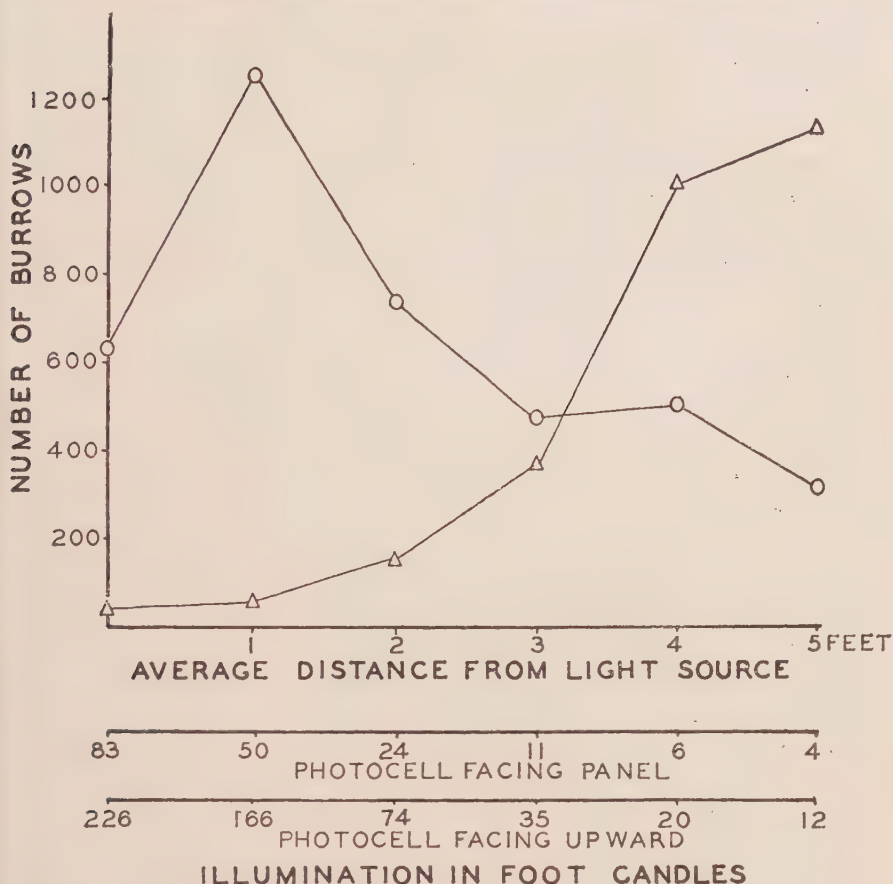


FIGURE 2. Distribution of borer attack on wooden panel of fourth experiment. Teredids indicated by circles, Limnoria by triangles.

of three or four days only, before they make their initial entry into wood. When first liberated, they swim actively by means of their velar cilia. During temporary cessations of ciliary activity the larvae sink slowly in the seawater. Observations upon larvae immobilized by reduced temperature and by killing with various agents show that they are of higher specific gravity than seawater of oceanic salinity.

In subdued light the larvae were observed to swim upwards until they reached the surface, when their activity was lessened. Occasionally they would sink passively through varying distances, only to

renew their ciliary action and return to the surface. The upwards movement was not always in a strictly vertical line, but would sometimes be at a steep angle or in a spiral. Occasionally larvae were observed to alter their posture and progress at an angle from the vertical of as much as 60° . Larvae which sank to the bottom of the vessel would swim back to the surface, crawl by means of the foot for short periods or remain inactive. During the first days of their free-swimming stage the crawling movement was resorted to infrequently. During the third and fourth day, however, crawling was predominant.

When placed in darkness for several minutes the greater number of larvae became concentrated at the surface, particularly in the earlier stages. This was quite clearly due to increased ciliary activity. When placed in strong light a large proportion, but not all, of the larvae would immediately cease their activity and sink passively. The passive sinking was interrupted by occasional bursts of activity, which would bring about a temporary movement to a higher level in the water. A more detailed account of larval behaviour and initial boring mechanism is being prepared for separate publication.

In the experiments to be described each batch of larvae, after being liberated naturally from the parent, was isolated. At measured intervals of time, batches of at least fifty larvae were removed and subjected to the experimental procedures. (Figures 3). In this manner the behaviour of the organisms was studied at all stages of their free-swimming existence. Prior to each experiment the larvae were kept in darkness for fifteen minutes.

It will be noted that the same batch of larvae was used in several successive experiments. While this introduces obvious complications, due to the possibility of reactions being modified by previous experience, it was not possible to obtain the great number of larvae of the same age which would otherwise have been required.

First Experiment. A series of observations was made upon larvae contained in a broad shallow vessel with unidirectional light impinging upon it from a low oblique angle. In each case one half of the light beam was shaded. (Figure 3). Various intensities of illumination were used and larvae were subjected to the procedure at different ages. Their distribution between the shaded and unshaded portions was found by counting them. This was recorded when successive counts showed no further change.

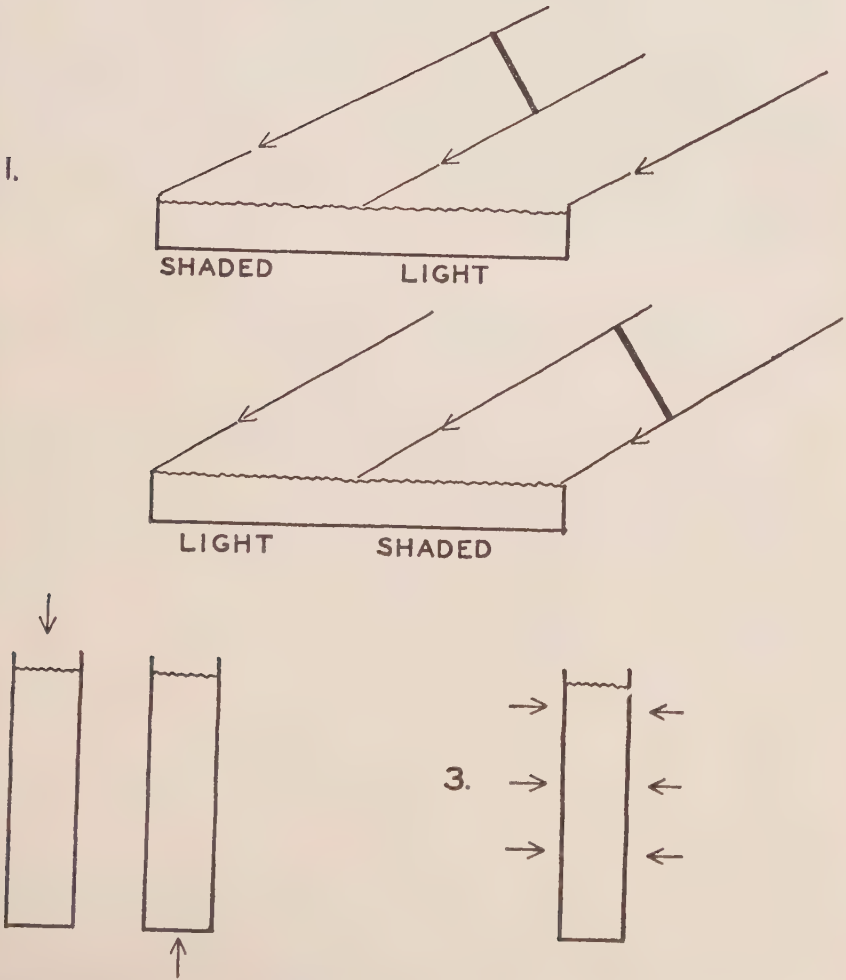


FIGURE 3. Diagram of arrangement for laboratory tests. (1) oblique unidirectional light. (2) Vertical unidirectional light. (3) Horizontal diffuse light evenly distributed around sides of tube.

Results of this experiment shows a mathematically significant tendency of larvae at all ages to become concentrated in the portion of the vessel furthest removed from the light source. (Table III). This tendency decreased with increasing light intensity and was slightly more marked when the lighted area was the furthest removed from the light source than when the shaded area was most remote, in the case of newly released larvae.

At light intensities above 270 foot candles this reaction was no longer apparent since the larvae were distributed without reference to light direction or intensity.

TABLE III
EFFECT OF OBLIQUE LATERAL LIGHT UPON HORIZONTAL DISTRIBUTION OF LARVAE. EXPRESSED AS PERCENTAGE OF LARVAE IN HALF OF VESSEL MOST REMOTE FROM LIGHT SOURCE.

LABORATORY EXPERIMENT I									
Light intensity foot candles		% LARVAE IN HALF MOST REMOTE FROM LIGHT SOURCE							
		Lighted half most remote from light source				Shaded half most remote from light source			
		Age of Larvae Since Liberation				Age of Larvae Since Liberation			
Lighted half	Shaded half	0	24	72	96	0	24	72	96
25	5	80	80	60	70	60	65	65	80
50	10	65	65	70	—	60	65	65	—
100	25	85	60	60	85	60	85	75	80
Average		77	68	63	77	60	75	68	80
270	50	65	65	70	60	65	65	70	60
350	50	34	34	56	50	40	40	64	54
600	100	46	40	60	64	28	28	36	60
600	250	30	58	32	54	44	40	58	48
600	350	48	48	72	48	38	38	52	56
Average		45	49	58	55	43	42	56	56

* Oct. 11, 1950.

Second experiment. The larvae were placed in a glass tube, so arranged that parallel rays of light could be directed in a vertical beam either from below or from above. After a lapse of time during which the organisms were observed continually, their distribution between the upper and lower halves of the tube appeared to remain constant and the numbers in each half were counted.

The results of this experiment (Table IV) show that, no matter whether the light source was above or below, the larvae tended to leave the upper part of the tube when illuminated. This tendency increased as the light intensity increased and also with increasing age.

TABLE IV
EFFECT OF VERTICALLY DIRECTED ILLUMINATION UPON THE DISTRIBUTION OF
LARVAE IN A VERTICAL COLUMN. EXPRESSED AS PERCENTAGE OF LARVAE
REMAINING IN THE UPPER HALF OF THE COLUMN*

LABORATORY EXPERIMENT II

<i>Intensity of Illumination foot candles</i>	<i>Direction of light Source</i>	<i>Age of Larvae since Liberation</i>			
		0	24 hours	72 hours	96 hours
5	above	65%	50%	30%	30%
	below	55	40	30	30
Average		60			
10	above	50	30	35	30
	below	50	25	25	30
Average		50			
20	above	25	20	25	10
	below	20	20	15	20
Average		22			
50	above	25	20	10	0
	below	20	20	10	10
Average		22			
70	above	15	20	10	3
	below	15	25	10	0
Average		15			
100	above	22	10	2	0
	below	20	14	2	0
Average		21			
250	above	34	20	2	0
	below	30	22	2	0
Average		32			
350	above	20	12	2	0
	below	18	10	0	0
Average		19			

* Oct. 12, 1950.

The only case where larvae were predominant in the upper part of the tube was when the illumination was less than five foot candles and the larvae were newly released. Movement to the lower part of the tube was due to decreased activity and therefore passive rather than active.

It was noticeable that, among the younger larvae, the tendency to leave the upper part of the tube when illuminated increased up to an illumination of about 70 foot candles and that above this intensity the behaviour continued to be the same. The older larvae, however, ceased swimming altogether at higher degrees of illumination.

The results indicate that the behaviour of all stages of the larvae does not necessarily depend upon the direction of the light rays. There was no significant difference between the disposition of larvae when the light source was below them and when the light source was above them.

Third Experiment. The larvae in this case were exposed in a vertical tube with diffuse illumination directed uniformly from all sides, but with no source of light on the top or bottom. (Figure 3).

The younger larvae showed generally similar tendencies to these in the previous experiment. (Table V). Increasing light intensity and increasing age of the larvae brought about a reduction in the proportion which remained in the upper part of the tube. Above an intensity of 250 foot candles, this effect was no less apparent and more larvae returned to the upper part of the tube. Older larvae of the batch used in this experiment were nearly all crawling and very few entered the upper part of the tube.

TABLE V

EFFECT OF LATERALLY DIRECTED ILLUMINATION UPON THE DISTRIBUTION OF LARVAE IN A VERTICAL COLUMN. EXPRESSED AS PERCENTAGE OF LARVAE REMAINING IN THE UPPER HALF OF THE COLUMN*.

LABORATORY EXPERIMENT III.

<i>Intensity of illumination foot candles</i>	<i>Age of larvae since liberation</i>			
	0	24 hours	72 hours	96 hours
5	55%	65%	4%	0%
20	35	20	0	0
50	19	14	2	0
100	14	40	2	0
250	8	16	4	0
350	24	58	0	0

* Oct. 11, 1950.

Fourth Experiment. The preceding experiment was repeated with either the upper half or the lower half of the tube shaded. In this case the decrease of larvae in the upper half of the tube with increasing light intensity was again noticeable. The 24 hour larvae, however, showed a greatly diminished tendency to leave the upper half of the tube, when illumination was confined to the lower rather than the upper half, at intensities of 5 to 70 foot candles. (Table VI). At higher illuminations the reverse was the case and more larvae left the

upper portion of the tube when illumination was confined to the lower part, than when it was confined to the upper half.

TABLE VI.

EFFECT OF LATERALLY DIRECTED ILLUMINATION UPON THE DISTRIBUTION OF LARVAE IN A VERTICAL COLUMN. EXPRESSED AS PERCENTAGE OF LARVAE REMAINING IN THE UPPER HALF OF THE COLUMN.*

LABORATORY EXPERIMENT IV.

Intensity of Illumination foot candles	Portion of tube illuminated	Age of larvae since liberation			
		0	24 hours	72 hours	96 hours
5	lower	45%	55%	20%	0%
	upper	20	15	15	0
10	lower	25	50	10	0
	upper	20	15	10	0
20	lower	20	35	10	0
	upper	20	15	20	0
50	lower	25	15	25	0
	upper	30	5	25	0
70	lower	20	10	20	0
	upper	25	6	20	0
100	lower	44	50	0	0
	upper	24	42	4	0
250	lower	10	30	0	0
	upper	10	38	2	0
350	lower	10	12	0	0
	upper	22	60	2	0

* Oct. 15, 1950.

Fifth Experiment. Experiments were carried out upon larvae which had lived a free existence for four days. They were placed in petri dishes upon thin slips of wood under conditions known to be favorable for boring. Light of intensity varying from 5 foot candles to 350 foot candles was directed upon them at various angles. In no case was tropotaxis noted. Movement was strictly localized and, apparently, random. The effect of exposure to light of various intensities upon the percentage of larvae which actually penetrate the wood was studied but no conclusive results could be obtained, due to the fact that only a small proportion of larvae finally enter the wood under laboratory

conditions. It is worthy of record, however, that successful boring took place over the entire range of light intensities to which the larvae were subjected.

DISCUSSION AND CONCLUSIONS

Results of the laboratory tests show a variation in the behaviour of individual larvae, since in no case did all of them respond in the same manner. Rather, a significantly larger proportion responded in a particular fashion and this proportion varied with intensity of the stimulus and with age of the larvae.

Larvae in the dark actively swam towards the surface in spite of negative buoyancy. This tendency was very marked in younger larvae and is referred to as a negative geotropotaxis, which decreases with increasing age of larvae.

Each group of experiments under conditions of increasing illumination was carried out upon the same group of larvae. This was desirable in view of the necessity of using a sufficiently large number of larvae in each experiment for the results to have significance. The effects of previous stimuli were, in so far as possible, overcome by keeping the larvae in the dark before each trial. Nevertheless this is recognized as a factor which may have entered into the results.

Under conditions of weak oblique light, in the first laboratory experiment, the majority of larvae became concentrated in the part of the vessel most remote from the light, irrespective of whether this area was more or less intensely illuminated than the part nearest to the light. This was clearly a case of negative phototropotaxis. The number of larvae responding in this manner decreased with the intensity of illumination and at intensities above 270 foot candles the response disappeared.

In the vertical tube, larvae remained at the surface only as a result of ciliary activity and sank when at rest. When exposed to vertically directed illumination they tended to sink passively to the lower part of the tube. Since this behaviour occurred no matter whether the light source was situated above or below and since the movement was passive, it must be considered the result of a negative photokinesis or inhibitory response, strong enough to overcome the negative geotropotaxis. (Table IV.)

Geotropotaxis was less marked in older larvae, since they were present in fewer numbers at the surface than younger larvae, under

conditions of weak illumination. In larvae of 72 hours or older the negative photokinesis increased its effectiveness in response to higher light intensities far more than in the young larvae, since at intensities above 70 foot candles, all activity ceased. (Table IV).

Similar results were obtained when the vertical tube was laterally illuminated, thus confirming the conclusion that a negative photokinesis is involved as well as the negative tropotaxis indicated by the oblique light experiment.

The oblique light experiment shows the effects of negative phototropotaxis, but it is reasonable to enquire whether this experiment should not also indicate existence of the negative kinesis. This would be expected to bring about a greater concentration of larvae at the end remote from the light source when that end was illuminated than when it was shaded. This was not apparent in the results. (Table III). It is believed that absence of this difference in older larvae may be explained by the nature of the negative kinesis. By actual observation it is known that, when illuminated, the larvae tend to cease their activity or change ciliary phase. There is no continuous cessation of activity however, but rather a tendency to relax for periods of time which become longer in duration and more frequent with increased intensity of light up to an optimum intensity of about 70 foot candles. (Table IV). Intermittent cessation of movement merely slows down the rate at which the larvae carry out their tropotactic movements in the horizontal dish and does not have any effect upon the final distribution ratio between the portions nearest to and most remote from the light source. This distribution ratio is merely an expression of the number of larvae which finally migrate away from the direction of the light source. (Table III).

Distribution of larvae in the vertical tube was explained on the basis of a negative photokinesis which tended to overpower their active upward movement or geotropotaxis. Nevertheless, the negative phototropotaxis, demonstrated in the oblique light experiments might be expected to modify the effects of this negative kinesis. If so, it should bring about a lower proportion of larvae remaining in the upper part of the tube when the light source was above than when the source was below. This did not occur to a significant degree. (Tables IV, V). Absence of this effect may possibly be due to relative weakness of the tropotaxis. According to this the tropotaxis would not

be noticeable in the vertical tube, where behaviour is mostly accounted for by the stronger negative kinesis. In the oblique light experiment, however, where, as shown above, negative kinesis is relatively ineffective, negative tropotaxis becomes evident.

Relative strength of negative kinesis compared to negative tropotaxis agrees well with the observed lack of any definite photoreceptor in the larval anatomy which is necessary for a directional response. The strongly negative photokinesis is also confirmed by the unpublished results of preliminary experiments in this laboratory which show decreased respiration of larvae when illuminated.

The fourth group of laboratory experiments showed at very low intensities of light, a greater decrease in negative geotropotaxis when the upper portion of the vertical tube was illuminated than when the lower portion was illuminated. This is readily explained on the supposition that larvae rising into an illuminated area would react by sinking passively. When the upper part of the tube is shaded, however, the larvae already in that portion would not be subjected to the influence of light and would remain there.

In the light of these results, behaviour of the teredid larvae may be summarized as follows. In younger larvae, vertical movement is basically a negative geotropotaxis. This activity is inhibited by a negative photokinesis which becomes most effective at light intensities above 20 to 50 foot candles. A weak tropotactic response to light, which is most effective in a range of illumination below 100 foot candles, brings about a horizontal movement away from the source of light, but does not affect vertical movement significantly.

At the stage when larvae are crawling and ready to begin boring they are indifferent to light.

It is difficult to interpret results of the panel experiments in terms of the foregoing. Since the larvae appear to be insensitive to light during their crawling phase, the distribution of borings with respect to light intensity would appear to depend upon the manner in which light affects distribution in the free swimming stages and the pattern of initial settlement.

The relative effectiveness of the negative kinesis and of the tropotaxis in distributing the free swimming stages under natural conditions depends in turn upon the effectiveness of the locomotor mechanism. A series of laboratory observations has shown the average speed of

swimming larvae to be 7.5 mm. per second or 1/60 mile per hour. This is greatly exceeded by the tidal currents at nearly all times of day or night in most natural conditions. In the foregoing panel tests the current of water through the test boxes was a minimum of 1/2 mile per hour. Under these circumstances it does not seem possible that a phototropotactic swimming movement of 1/60 mile per hour could be effective in the selection of a surface for settlement.

The negative photokinesis or inhibitory effect of light, demonstrated by the laboratory experiments appears to be a more suitable mechanism for varying the pattern of distribution settlement. Under conditions of illumination favoring ciliary movement the larva would tend to continue its swimming movement if, by chance, it encountered a suitable surface for settlement. If, on the other hand, the illumination was such as to inhibit swimming activity, the larva would more probably remain on a chance encountered surface. The negative photokinesis was found in the case of older larvae, to increase with increasing illumination up to a maximum at between 70 and 100 foot candles (Table II), with little movement occurring above this intensity. On the basis of the mechanism suggested above, this would result in increased settlement with increasing light intensity, with a maximum at 70-100 foot candles. The number of borings on the panels did, in fact, increase with increasing illumination. The decrease in number of borings above 166 foot candles illumination in the panel experiments is not readily explained, however.

A possibility which occurs is that the inhibitory effect of light does not reach a maximum with cessation of ciliary activity, but that in stronger light the activities involved in settlement upon a surface may also be inhibited. No evidence of this was noted in the present experiments. The observations by no means precluded such a possibility, although once the larva was settled, crawling was not visibly affected by light. Should the activity involved in initial attachment to a surface be inhibited when light intensity increases above, for instance, 166 foot candles, this would satisfactorily account for the results of the panel tests.

Applying the experimental results to the behaviour of teredid larvae under natural conditions it is reasonable to assume that, under conditions of darkness larvae will concentrate at the surface of the water. During day time they will be dispersed and in the stronger

light of open water will tend to remain in the deeper less illuminated water. In the shade of docks they will rise. Settlement and subsequent boring may be expected to occur at a maximum under conditions of illumination in the order of 160 foot candles. This represents deep shade, since illumination at the surface of open water on a bright day is in the order of 20,000 foot candles.

The behaviour of *Limnoria* larvae in the panel experiments shows a significant decrease in attack with increasing light intensity. This is in complete agreement with the observations of Henderson (1924) upon the distribution of *Limnoria* attack at St. Andrews Bay.

Because of the great difficulties inherent in culturing and handling large numbers of larvae it has not been possible to achieve results in the above experiments which allow of any but tentative conclusions. It is believed, however, that sufficient data has been presented to indicate that the behaviour of teredid larvae is of a more complicated nature than the simple tropism to which behaviour in similar organisms has been customarily referred.

SUMMARY

1. Experiments were carried out upon larvae of *Teredo pedicellata* under laboratory conditions, using light of variable intensity, both diffuse and unidirectional.

2. The results indicate that, in darkness, larvae are negatively geotropotactic. When illuminated the behaviour is modified by a weak negative phototropotaxis and a stronger negative photokinesis which reaches a maximum at about 70 foot candles in younger larvae. Older larvae cease swimming altogether in this intensity of illumination. Illumination has no apparent effect upon older larvae while crawling upon wooden surfaces.

3. Wooden panels suspended in sea water and subjected to varying intensities of illumination show a maximum amount of teredid attack when subjected to 166 foot candles. At higher and lower intensities of illumination the number of borings decreases. *Limnoria lignorum* burrows are most numerous at low intensity and decrease in number with increasing intensity of light.

4. The significance of these results is discussed in their relation to the pattern of borer attack under natural conditions.

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A first record of the Cephalopod,
Scaevrgus unircrrhus, from the Western Atlantic¹

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THESE NOTES on the octopod *Scaevrgus unircrrhus* (Orbigny) are based on three specimens received from A. R. Thompson and T. L. and P. L. McGinty who took them in a series of dredgings made by Mr. Thompson's yacht "Triton" along the lower Florida coast during the summer of 1950. They were obtained with small steel dredges in depths of from 40 to 85 fathoms from the lower Florida Keys to Palm Beach. They are especially remarkable as being the first specimens of this genus to be recorded from the Atlantic Ocean. Their former known range was restricted to the Mediterranean Sea, the Indian Ocean, Japan, and the Hawaiian Islands.

Family OCTOPODIDAE Orbigny

Subfamily Octopodinae Grimpe

Genus *Scaevrgus* Troschel

Scaevrgus unircrrhus (Orbigny)

Syn. ref.

Octopus unircrrhus Orbigny, 1840, p. 70, (orig. descrip.).

Scaevrgus unircrrhus, Robson, 1929, p. 192 (contains detailed synonymy).

FLORIDA MATERIAL

1 male, juv. (alcohol), from "85 fathoms, SE of Sombrero Light (shell and mud) June 12, 1950." Author's catalog No. 38.

1 female, (alcohol), from "off Breakers Hotel, Palm Beach, Fla. 40 fathoms. Triton Sta. 195, July 28, 1950." Author's catalog No. 37.

1 female, (alcohol), from "50 fathoms off Palm Beach, Fla. (sand and shell) Triton, August 2, 1950." Author's catalog No. 39.

This is a rather small species (Fig. 1) with a short, thick, compact body and head, and rather prominent eyes. The arms are subequal, of moderate length, armed with small suckers arranged biserially. The web is deep and subequal. The body is covered uniformly with round papillae which quite often tend to be arranged in linear fashion and in parts of the body are fused into ridges. This occurs notably at the base of and on the arms, at the corners of the

1. Contribution No. 51, Marine Laboratory, University of Miami.

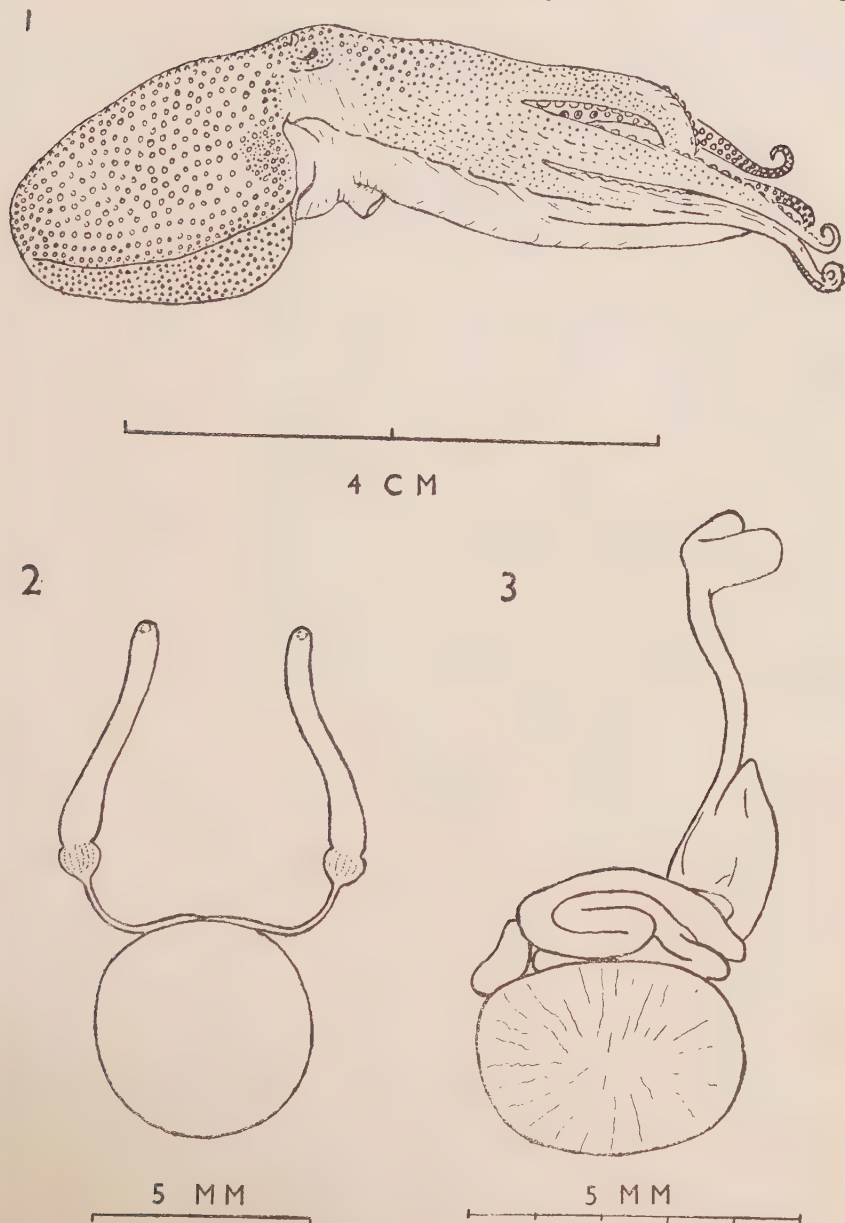


FIGURE 1. Side view of female of *Scaevargus unicirrhus* (Orbigny) from Florida. FIGURE 2. Female genital organs. FIGURE 3. Male genital organs.

pallial aperture, and around the periphery of the mantle where they form a distinct keel which terminates apically in a large soft papilla. There is a single multifid cirrhus over each eye, although in one specimen this is preceded by a smaller one.

The color (in alcohol and examined within two weeks of capture) is reddish brown to brownish yellow dorsally, marked with chocolate mottlings. The ventral and oral surfaces are pale yellowish brown.

There are 12 to 13 filaments per demibranch of the gills. The visceral mass is contained within a semi-transparent integument which bears numerous small brown chromatophores. The female genitalia (Fig. 2) consist of a large, disk-shaped ovary placed apically, and a short, small proximal oviduct which terminates in a small round oviducal gland. The distal oviduct is comparatively large and long.

The male genitalia (Fig. 3) are similar to those of *Octopus vulgaris* but the penis has the characteristically long diverticle. The hectocotylyzed arm of the juvenile male is not fully developed. The ligula is only weakly developed and small, and the calamus is not evident.

Table I.—Measurements (in mm.) of one juvenile male and two adult females of *Scaevargus unicirrhus* (Orbigny) from the SE coast of Florida.

SEX	MALE		FEMALE		FEMALE	
Author's register	38		37		39	
Total length	50.0		70.0		73.0	
Mantle length	16.0		25.0		24.0	
Mantle width	15.0		20.0		19.0	
Head width	12.0		15.0		13.0	
No. of gill filaments	12		12		13	
Web, max. depth	10.0		16.0		20.0	
Sucker, max. diam.	1.0		1.5		1.2	
Arm width	3.0		4.0		3.5	
ARMS, LENGTH	L	R	L	R	L	R
1st pair	34	33	42	42	45	44
2nd pair	34	34	44	43	47	—
3rd pair	30	33	44	43	48	48
4th pair	32	32	43	42	45	46
Web depth A sector	9.0		11.0		16.0	
Web depth B sector	10.0		14.0		18.0	
Web depth C sector	10.0		16.0		19.0	
Web depth D sector	9.0		13.0		20.0	
Web depth E sector	8.0		13.0		18.0	

OCCURRENCE. This species was originally described from the Mediterranean Sea, and Jatta states that it is littoral in habit, being found to a depth of 50 m. on muddy bottom. Robson (1921) records it from the Indian Ocean. Berry (1913) described *S. patagiatus* (see discussion below) from Hawaii and gives the depths as from 127 to 178 fathoms (Berry 1914) and the bottom as composed of gray sand and foraminifera. Sasaki (1920) records *S. patagiatus* from off Kyushu, Japan in 159 fathoms. The new Florida records are from 40 fathoms (no bottom record given), 50 fathoms (sand and shell), and 85 fathoms (mud and shell).

The fact that the juvenile male was taken on the Pourtales Plateau, an oceanic shelf on the western side of the Gulf Stream having its origin in the vicinity of Key West and extending to the northeastward to Carysfort Reef, indicates that it is probably native to the Gulf of Mexico as well. The two areas have many similarities in their benthic fauna, and many gasteropod mollusks found on the Pourtales Plateau are also found in the upper Gulf of Mexico. *Octopus burryi* Voss (1950) which was found in this same locality has since been taken in 38 fathoms off the Mississippi Delta by the U. S. Fish and Wildlife Service vessel "Oregon." The specimen, a male, was sent to me for identification by Harvey R. Bullis Jr. and a description of this specimen with notes on the species will be published shortly. At the same time the occurrence of the two females of *S. unicolorrhynchus* far to the northward suggests that they may also occur well up the Atlantic coast.

DISCUSSION. The genera *Scaevargus* and *Pteroctopus* are remarkable among the Octopodinae due to the modification of the third left arm for copulation instead of the third right as is characteristic of the Octopodinae in general. It is also closely allied according to Robson (1929) to the genera *Joubinia* and *Enteroctopus* by the possession of a long penial diverticle in the male system.

Under the old classification the genus *Scaevargus* contained three species; *S. unicolorrhynchus*, *S. tetracirrhynchus*, and *S. patagiatus*. Robson (1929) pointed out that *S. tetracirrhynchus* differed from *S. unicolorrhynchus* so markedly that he followed Fischer (1882) and placed it in the genus *Pteroctopus*.

Robson (1929) in his review of the genus, working with specimens in the British Museum from the Mediterranean Sea and the Indian Ocean, and from the data given by Berry, placed *S. patagiatus* in the synonymy of *S. unicolorrhynchus* but at the same time made several quali-

fying remarks as to this position. It is indeed unfortunate that neither Berry nor Robson had access to specimens of both species. At the same time it should be pointed out that so few specimens of *Scaeur-gus* are known over its world wide range that a collection for a study of this sort is difficult to obtain.

Berry (1914) noted this difficulty, and as at that time the known range was very limited, considered his specimens as a new and separate species. In a personal communication he states "in view of the antipodean distribution, there seemed no other sound recourse for the Hawaiian form than to assume distinctness for it." In connection with this confusing situation when the Florida material came into my hands, the opportunity presented itself to make a close and detailed examination and comparison of Berry's paratypes and this material. Thanks to the kindness of Dr. Harald A. Rehder of the U. S. National Museum the Hawaiian paratypes were made available and it was possible to remeasure Berry's material. The specimens were in excellent condition and shrinkage over a period of some thirty-five years had been so negligible that nearly all of the present measurements coincided with those originally given by Berry. A few additional measurements were taken and with this data the following table, No. II, was compiled using the indices as defined by Pickford (1945).

Table II.—Measurements and indices of three Florida and three Hawaiian specimens of *Scaeur-gus unicolor*.

SEX	Florida Specimens			Hawaiian Specimens		
	MALE	FEMALE	FEMALE	MALE	FEMALE	FEMALE
Total length	50.0	70.0	73.0	60.0	97.0	130.0
Mantle length	16.0	25.0	24.0	19.0	22.0	34.0
Mantle width	15.0	20.0	19.0	15.0	18.0	28.0
Head width	12.0	15.0	13.0	10.0	11.0	19.0
Mantle width index	93.7	80.0	79.1	78.9	81.8	84.7
Head width index	75.0	60.0	54.1	52.6	50.0	55.9
Sucker index, normal	6.0	6.0	5.0	6.2	6.8	9.0
Arm length (longest arm)	34.0	44.0	48.0	37.0	60.0	90.0
Arm length index	66.6	62.8	65.0	61.6	61.8	69.2
Mantle—arm index	47.0	56.0	50.0	51.6	36.6	35.5
Arm width index	18.7	16.0	14.5	13.6	13.6	13.2
Web depth index	29.4	36.0	41.6	35.0	30.0	30.0
No. of gill filaments	12	12	13	12	12	12

A further comparison can be made on some points using the index ranges for the specimens examined by Robson (1929, p. 54) from the British Museum.

Table III.—A comparison of some length and index ranges of some specimens from the British Museum, Florida and the Hawaiian Islands.

<i>Specimens</i>	<i>Mantle length</i>	<i>Mantle width index</i>	<i>Head width index</i>	<i>Arm length index</i>
British Museum	43-56	70-90	50-60	
Hawaiian	19-34	79-85	50-56	62-69
Florida	16-25	79-94	54-75	63-67

Tables II and III give the comparative measurements so well that no additional remarks seem necessary since the two groups examined fall well within the ranges of the indices. The major discrepancy appears in the arm width index, but this apparently is due to preservation rather than to a real difference in the specimens themselves. The arm order is very variable in all of the specimens, but on the average the second pair of arms is the longest and the first or fourth pair is the shortest. The web depth order is similarly uncertain, but again on the average sectors C and D are the deepest and A and E are the shallowest, usually A. The mantle aperture is very wide (C) in both the Florida and the Hawaiian specimens, although Robson (1929) states that in the specimens from the Mediterranean Sea and the Indian Ocean it is narrow.

All of the Florida specimens show the characteristic ridge about the periphery of the mantle as described by Berry (1914) and also the ridges from the mantle aperture to the ends of the arms, although these are mostly confined to the third pair of arms as they are in the specimens of Berry's examined by me.

The genitalia of all of the specimens were very closely examined and compared but no difference could be detected. In the Florida female of 25.0 mm. in mantle length, the ovary was 5mm. in diameter with a small proximal oviduct 3.5 mm. in length and .25 mm. in diameter. The oviducal gland was .9 mm. long and 1.05 mm. wide and separated from the distal oviduct by a slight constriction, and appeared to be longitudinally striated. The distal oviduct was 5 mm. long and .75 mm. in diameter. One of the females was gravid, containing very small immature eggs.

The male genitalia in both specimens showed the characteristic long penial diverticle, although in the Florida male the diverticle had become turned in and folded down against the penis in preserva-

tion and both were considerably flattened. The ligula in both the Florida and the Hawaiian juvenile males is not fully developed, there is no sign of a calamus, and the spermatophoral groove is not fully formed. In neither was there any sign of the infolding on the sides of the ligula, nor were there any indications of any enlarged copulatory suckers. Berry, however, states that he found specially enlarged suckers on one or both of the other males examined by him.

REMARKS. From the preceding discussion and tables it appears certain that *Scaevurgus unicirrhus* (Orbigny) and *S. patagiatus* Berry are identical and that the species is world-wide in distribution. It seems remarkable that the specimens of a benthic species from the Atlantic and Pacific Oceans agree so perfectly with one another. Dr. Berry (personal communication) states, in relation to this problem, "if it really is all one species, then there must be some special reason for the lack of divergent speciation, and I can conceive no sensible explanation for this in a creeping bottom form except the possession of a planktonic larval stage of some duration."

Degner (1925, p. 79) refers the specimens of *Macrotritopus*-like young octopods taken in the Mediterranean to the genus *Scaevurgus* as he found traces of hectocotylization on the third left arms. If this is correct and other larval forms of this type are ascribable to *Scaevurgus* then this may be the answer to the wide distribution of the genus. However, Robson (1929, p. 168) failed to find signs of a hectocotylus on the males examined by him and I have likewise been unsuccessful in a study of a small series of larval forms which I consider to be the *scorpio* form described by Berry (1920, p. 299) from the western Atlantic. Even so, the small size of the eggs suggests a long larval stage such as is represented in *Octopus vulgaris* whose larval forms are commonly found in the plankton of the Gulf Stream off the Florida coast.

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Histopathology of Infection of *Crassostrea virginica* (Gmelin) by *Dermocystidium marinum*

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ALTHOUGH MASS MORTALITIES of oysters suspected or known to be caused by disease have been reported by various authors (Needler, 1931; Orton, 1924; Korringa, 1947; Roughley, 1926), at widely separated points in the world, few studies have been made of the pathology of infection by a known organism. Roughley (1926) described and figured abscesses in diseased tissues of oysters without determining whether or not an invading organism was present. Prytherch (1940) described degenerative effects of adductor muscle fibers resulting from heavy infections by *Nematopsis ostrearum*, a gregarine parasite. Orton (1924) recorded a high percentage of pale-colored livers, and discussed myolysis in diseased oysters but without coming to any conclusion as to the cause of the muscular degenera-

All figures are photomicrographs

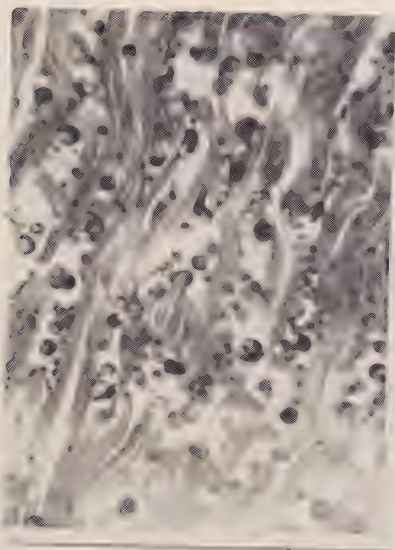
Fig. 1. *D. marinum* in adductor muscle of oyster, to show nature of parasite. This section was selected because of the few leucocytic cells present and shows the spherical nature of the parasitic cells, the eccentric vacuole and inclusion body contained therein. Lysed cavities are evident. Delafield's haematoxylin and eosin. Original magnification about 950 diameters.

Fig. 2. Inflammation of the intestinal epithelium and connective tissues underlying the basal membrane due to concentrations of leucocytic cells. Only moderate infection of the epithelium and few parasites have invaded the connective tissue. Delafield's haematoxylin and eosin. Original magnification about 400 diameters.

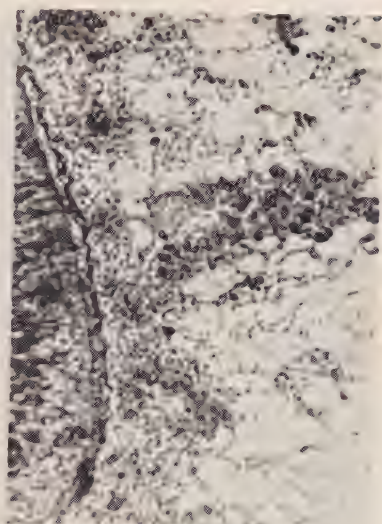
Fig. 3. Normal intestinal epithelium. This oyster was parasitized locally (see Fig. 4) and some tissue response and congestion is to be seen in the connective tissues. Harris' haematoxylin and eosin. Original magnification about 100 diameters.

Fig. 4. Abscessed intestinal epithelium of the same oyster as that shown in Fig. 3, the section through a different loop. Note thickening of the epithelium, the numerous characteristic round cavities containing the parasitic cells, separation of the basal membrane from the underlying connective tissue, destruction of the ciliated border and leucocytic infiltration. Harris' haematoxylin and eosin. Original magnification about 100 diameters. Compare with Fig. 3.

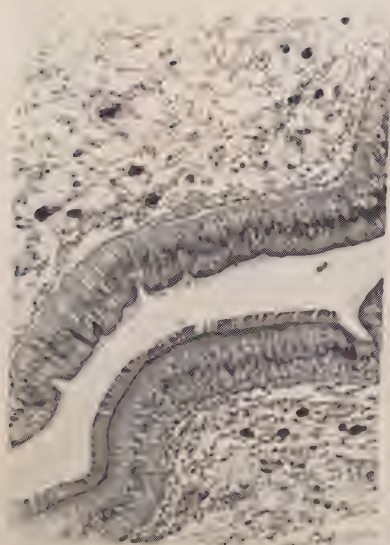
1. Contribution No. 4 from the Department of Oceanography of the Agricultural and Mechanical College of Texas.



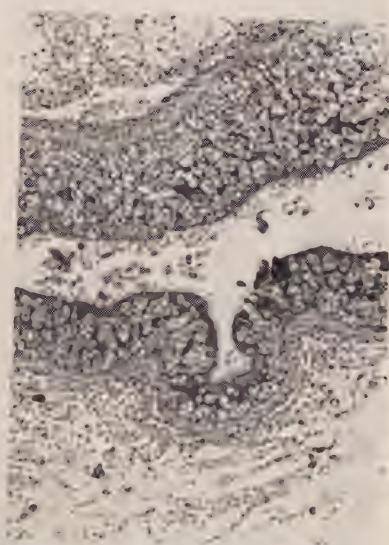
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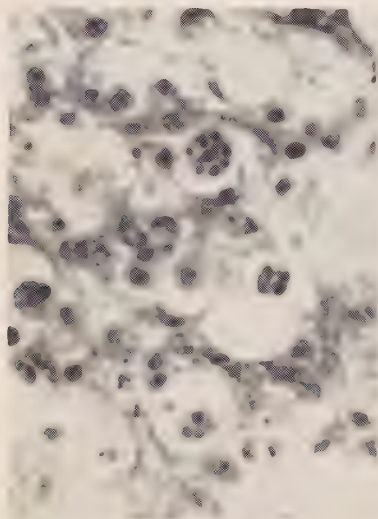
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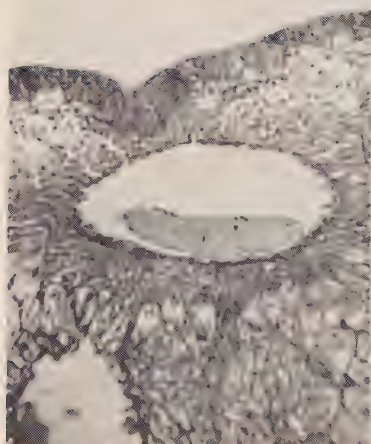
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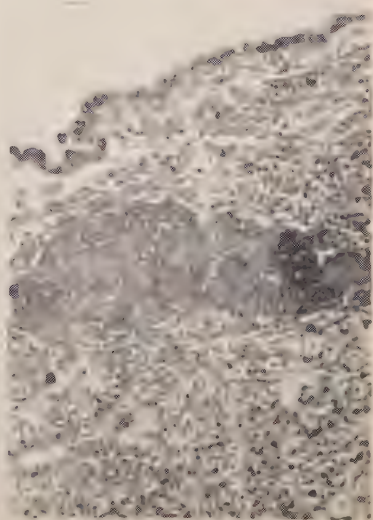
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tion. He also noted pathological conditions in stomach epithelium and in connective and reproductive tissues, as well as cyst formation. Although Orton failed to find a cause for the pathological conditions described, he figured what are undoubtedly parasitic cells closely resembling certain Sporozoans. His figures also show extreme leucocytosis in tissues underlying the stomach epithelium and in blood spaces, but he did not discuss the pathological processes related to such concentrations. In one figure Orton shows "blood cells" which are smaller in average size than the nuclei of adjacent cells, which prompts the suspicion that he actually observed concentrations of parasites. Korrington (1948) described hypertrophy and consequent abnormal secretion of cells of the mantle epithelium induced by a shell-boring fungus. Giard (1894) in discussing the "maladie du pied" called attention to the degeneration of the shell attachments of the adductor muscle fibres, and attributed the general atrophy to attacks of a Schizomycete, *Myotomus ostrearum*, a conclusion somewhat doubtful in view of the nature of the studies made. Needler and Logie (1947) described abscesses, tissue breakdown, and general emaciation resulting from a disease of unknown etiology in oysters of Prince Edward Island, Canada. In general, details have been lacking in all of these studies and in most cases either no associated parasite was indicated or the etiology was in doubt. In no case is there evidence that systematic comparison of pathologic conditions with normal tissues was a part of the studies.

Fig. 5. A small section of diseased epithelium from the abscessed area shown in Fig. 4 more highly magnified. Note the lysed cavities and reproductive stages of the parasite. Original magnification about 950 diameters, greatly enlarged.

Fig. 6. Section through a portion of the digestive gland of a normal oyster with no infection, showing tubule and supporting connective tissue with a small blood vessel. Heidenhain's haematoxylin and eosin. Original magnification about 400 diameters.

Fig. 7. Section through the margin of the mantle of a normal, uninfected oyster to show one of the large blood vessels with radiating fibrous connective tissue, epithelium, and Leidig-cell basal connective tissue. Heidenhain's haematoxylin and eosin. Original magnification about 220 diameters.

Fig. 8. A portion of necrotic mantle to show amorphous basophilic mass resulting from what appears to be liquefaction of tissue resulting from combined auto-digestion of disintegrating cells and lytic action of larger numbers of parasites. Delafield's haematoxylin and eosin. Original magnification about 220 diameters.

This paper presents data on the pathologic changes in various tissues of *Crassostrea virginica* associated with infection by *Dermocystidium marinum* Mackin, Owen, and Collier (1950) a recently discovered Protistan. It is characteristic of this parasite that massive infections are built up in the host. Large numbers of oysters in Barataria Bay, Louisiana, and adjacent areas are infected during high temperature months, providing an excellent opportunity, because of abundance of material, to make a detailed study of histopathological changes related to various stages of infection.

Researches on the diseases of oysters, as well as on many other phases of oyster biology, have been supported by The Texas Company, Humble Oil and Refining Company, The California Company, Tidewater Associated Oil Company, Phillips Petroleum Company, Shell Oil Company, and Gulf Refining Company. The author wishes to make grateful acknowledgement not only for past and continuing financial support, but also for helpful collaboration in every possible way. Due also to my colleagues of the Texas A.&M. Research Foundation is acknowledgement of active collaboration. Dr. Sewell H. Hopkins has carried the burden of library search and direction and counsel. Fred Cauthron and Joe Prokop have made all photomicrographs, and slide techniques and related laboratory work has been largely the work of Dan Wray and J. L. Boswell. Many others have contributed materially. Interpretations of the data are the responsibility of the author.

MATERIALS AND METHODS. Sections of more than 1000 oysters have been made and studied. Many of these are not usable for histologic study because of degeneration of tissue at death of the host. Oysters used came from several sources. These were as follows: (1) from 17 oyster experimental field stations in Barataria Bay, Louisiana, and adjacent waters of the same region, (2) from laboratory experimental tanks at the Grand Isle Laboratory of the Texas A.&M. Research Foundation, (3) from various planted oyster beds in Barataria Bay and vicinity, (4) from several points on the Atlantic coast of the United States and points on the Gulf Coast outside of Louisiana. These include oysters from Delaware Bay (New Jersey); Rappahannock and James rivers, Virginia; Charleston, South Carolina; Pensacola, Florida; Gulfport, Mississippi and Aransas Bay, Texas. In addition, sections of *Ostrea edulis* (France and Holland), *Ostrea equestris*

(Texas Gulf Coast), and *Crassostrea commercialis* (Australia) have been studied. Outside of Louisiana *Dermocystidium* has been found only in the Virginia rivers, South Carolina, Florida, and Mississippi.

Fixation of oysters has been by (1) Zenker's fluid, (2) Bouin's fixative, (3) 10% formaldehyde, (4) Schaudinn's fluid, and (5) Helly's fluid. Only Zenker's fluid gave consistently satisfactory results. Oysters in nearly all cases were fixed *en toto*; those cut into smaller pieces before fixation showed little advantage. Transverse blocks were cut from the fixed oysters and sectioned and a variable number of slides were made from each block; the sections were oriented to give a transverse section of the visceral region in the vicinity of the base of the palps. Some of these included palp tissue and some gill tissue, some both types, in addition to others which would always be included in such a section. Many oysters were sectioned through the ventral part of the adductor muscle and tissues ventral to the muscle, which included the lower loops of the intestine and style sac, renal epithelium, and posterior margin of the gonads. A special study was made of the heart and visceral ganglion. Additionally many sections were made of other organs or regions for special purposes.

Both living and dead oysters were fixed and sectioned. The live ones varied widely in concentration of infective elements from negative, of which there were many, through light, moderate, and heavy infections. Many of these "live" oysters were actually gapers (i.e., too weak to effect closure of the shell by the adductor muscle) but with ciliary movement, mantle sensitivity, or weak heart beat to attest to the living condition of the tissues. These still-living gapers provided the best material for study of the effect of massive infections. For experimental purposes such oysters are classed as dead, for they never recover if heavily infected with *Dermocystidium*. Oysters actually dead when recovered are of little value for histological study, since it is impossible to make interpretations from dead tissues. Many such oysters were sectioned, and most were in good enough condition to allow determination of the degree of infection and were valuable in that connection. Some few were so far disintegrated by the action of saprophytic bacteria that they were useless for any purpose.

Several hundred oysters with moderate to heavy infections were stained with a Gram stain to determine the incidence of bacterial invasions. These latter were rare and were associated with degenerative

changes taking place after death. A few oysters showed actual parasitic invasions with bacteria as complications of infection with *D. marinum*. Such complications were easily separable in effect from the primary infections. A few cases of primary bacterial parasitization of live oysters without *D. marinum* infection were recorded. Additionally several other diseases of oysters are present in Barataria Bay and appeared in sections in various percentages of the specimens.

NATURE OF THE PARASITE. A preliminary description of *D. marinum* has appeared in Science (Mackin, Owen, and Collier, 1950). It need only be noted here that the parasite is believed to be a fungus and the only known stages are small spherical vacuolated cells (Fig. 1), which reproduce prolifically in the oyster tissues by a schizogony-like process closely resembling that of certain Sporozoans. The cells of *Dermocystidium* are morphologically somewhat like those of the human blastomycosis-producing organisms such as *Blastomyces* and *Cryptococcus*. Infective stages are not known, nor has production of anything resembling a mycelium been observed. So far as now known *Crassostrea virginica* is the only host.

HISTOLOGICAL CHANGES ASSOCIATED WITH *Dermocystidium marinum* INFECTION IN *Crassostrea virginica*. For purposes of discussion three stages of infection with *D. marinum* may be recognized. Light infections are defined as those in which the distribution of parasitic cells is such that search is necessary to confirm infection. A moderate infection is defined as one in which local foci of infection have developed to the point where a number of parasitic cells are concentrated in localized areas of tissue, producing obvious histologic changes, but in which a large part of the host tissue has not been infiltrated. A heavy infection is one where the major part of all tissues excepting certain epithelia are more or less heavily infiltrated and at least some areas contain massive infections.

Several basic characteristics of *D. marinum* infections should be noted at this point. First, any tissue is susceptible to invasion although even in heavy infections the external epithelia and peripheral nerves are not usually penetrated. Second, infection during high temperature months and in high salinity waters proceeds to the point where it can only be described as massive. In development of massive infection as well as in some other respects *Dermocystidium* disease resembles human blastomycosis (Gilchrist's disease). For an account of this

latter see Conant, *et al.*, (1944). Third, the damage done to host tissues results largely from lytic action of the parasitic cells, coupled with embolism in late stages. There is apparently no marked toxic action judging from the sometimes extreme concentrations of parasites built up before death of the host.

Light infections of *D. marinum* are usually to be found only in the digestive epithelium and may be distributed from the stomach to the rectal region. In some slides, occasional cells may be found in the mantle connective tissue when there are none in the digestive epithelium, but it is considered likely that in these cases sections of the digestive tract in body regions other than the standard anterior visceral location would have shown a primary infection. However, this is by no means a certainty in all cases and it is distinctly possible that infection may take place through any epithelial surface.

The first reaction to infection is a marked leucocytosis and the usual migration of phagocytic cells to the site of parasitic lodgement, resulting in inflammation (Fig. 2). Leucocytes invading the digestive epithelium often are in such numbers that displacement of columnar epithelium may be extensive as shown in Figure 2. Masses of leucocytic cells accumulate in the connective tissue under the basement membrane even when few parasites have migrated from the digestive epithelium.

After establishing a primary focus in the digestive epithelium, an extensive abscess may be produced by development of large numbers of parasites. Normal intestinal epithelium is composed of tall columnar cells, closely packed and with nuclei distributed near the middle. The ciliated border is sharply defined (Fig. 3). Extensive infiltration of the epithelium results in (1) infiltration by leucocytes (2) destruction of epithelium and leucocytes alike by lytic action of the parasites and (3) destruction of ciliated border (Fig. 4). Separation of the basal membrane from the underlying connective tissue often takes place and the resulting cavity fills with leucocytic and also parasitic cells if the basal membrane has been penetrated by the latter (Fig. 4). Figure 5 is a greatly enlarged portion of Figure 4 showing the development of parasites in lysed cavities characteristic of *Dermocystidium marinum* infection.

Such heavy concentrations as shown in Figure 4, ultimately result in liberation of the parasites into the lumen of the digestive system. Large areas of the epithelium are sloughed off from the basement

membrane, and the necrotic tissue and parasites fill the lumen. They also gain access to the connective tissues through lysis of the basement membrane. Once in the connective tissue mesenchyme, distribution to all parts of the body takes place through the medium of the blood sinuses and large veins and arteries. In advanced stages of disease numerous parasites and leucocytes may completely obliterate the sinuses and obstruct all but the largest blood vessels.

The connective tissue, especially in the digestive gland region, mantle, and gills, is peculiarly susceptible to attack. Connective tissues in the oyster consist of large Leidig cells, which are derived from modified leucocytic cells, and localized areas of fibrous tissues, which are especially marked about the walls of blood vessels. In *Crassostrea virginica* the yellowish "pigment" cells are sparingly distributed throughout the connective tissues but are concentrated in the auricle of the heart and to a lesser extent about the basal membrane of the digestive system throughout its length. Figure 6 shows connective tissue supporting tubules of the digestive gland in a normal oyster. A small amount of fibrous tissue is radiating from the small blood vessel. Figure 7 shows normal connective tissue composed of radiating fibers and Leidig cells around a large blood vessel in the mantle.

Infiltration of connective tissues results in either (1) generalized evenly distributed infective elements ultimately resulting in conversion of the entire visceral mass into one large abscess (Figs. 8 and 9), or (2) more localized infection producing small abscesses (Figs. 10, 11, and 12). This latter condition is often encountered in the mantle. Sections here often show numerous pinhead-size abscesses filled with tissue debris, parasites, and leucocytic cells. These tend to lie close beneath the mantle epithelium and to destroy tissues of the basement membrane resulting in atrophy, necrosis, and ultimate sloughing of the epithelium (Fig. 11), a process which converts abscess to ulceration.

Several specific pathologic responses to infection of the connective tissues should be noted. First is the usual development of marked fibrosis especially well shown in Figures 11 and 12. In late stages much of this fibrous material may be lysed and the fibroblasts destroyed. Second is the production of a caseous-like deposit resulting from liquefaction of the host tissues in the abscess (Figures 8, 10, and 12). The staining reaction of this amorphous material is often distinctly baso-

philic. Third is the tendency of the so-called pigment cells to increase in numbers. These cells are probably of leucocytic origin and contain deposits of yellowish granules. During infection with *D. marinum* their number is greatly augmented and they appear in tissues and areas where they are normally rare (Fig. 9). The granules stain black with Heidenhain's haematoxylin and dark green with Giemsa. Augmentation of pigment cells has become a valuable pathologic index. The nature of the granules is unknown but it is suggested that it may be some type of metallic deposit of the general nature of haemosiderin.

Phagocytic activity of leucocytic cells results in ingestion of large numbers of parasites which grow and reproduce intracellularly as well as in lumina of cavities. It is common to find parasites in well over 50% of the leucocytic cells which invade infected tissues. Ultimate destruction of all parasitized leucocytes is probable and it is certain that few escape. *D. marinum* cells develop vigorously in the cytoplasm, pushing the nucleus to the periphery, and the cell is represented finally by only a thin shell which ruptures to liberate the parasites. Much of the cellular debris seen in tissue abscesses results from breakdown of leucocytes. In heavy infections diagnosis may often be accomplished by examination of fluid from the pericardial cavity, which may contain enough cells to produce a decided turbidity. Parasites are clearly seen in fresh unstained mounts of such fluid as dark bottle-green rounded inclusions in the moribund leucocytes. Much tissue debris is also contained in such material (Fig. 13).

Concentrations of parasites may often also be found in the fibrous wall of blood vessels, especially of the mantle. Increased deposit of fibrous tissue and invasion by leucocytic cells is the first response to the presence of parasites, and an abnormal thickened appearance of the wall of the vessel results (Fig. 12). Ultimately this tissue is lysed to the extent that the vessel as such no longer exists as a containing vessel and it is difficult to distinguish a cross sectional view from an abscess. Although the heart itself is often affected, complete breakdown of the walls is unusual, and in general the trabeculae are apt to be more lightly infected than are the fibrous walls of peripheral vessels. Circulatory failure is probably one of the most common immediate causes of death of the host.

Transportation of infective cells from primary foci to the adductor muscle is probably via the posterior aorta. Massive infection of part or

all of the adductor muscle is a common occurrence. Longitudinal sections through the muscle give the best picture of the gross pathological results of such infections. Figure 14 is a section of normal bundles of fibers with intervening blood sinuses. Figure 15 shows a section of heavily parasitized muscle with masses of infiltrated leucocytes. Apparently the primary action is destruction of the fiber sheaths and terminal attachments, and individual fibers lie in haphazard and twisted masses. Individual released fibers become the myolytic spindles of Orton (1924) and are often carried by the blood stream to remote parts of the viscera. A muscle such as shown in Figure 15 is soft and mucoid to the touch, and heavily infected parts retain little or no attachment to the shell. Extensive involvement of the adductor muscle results in gaping. Muscles of the mantle are also subject to lysis.

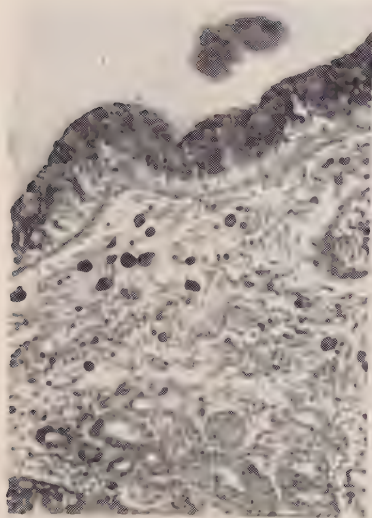
Marked effect of infection on tubules of the digestive gland always results from infection of the supporting connecting tissues. Epithelia of the tubules themselves are not usually attacked, but destruction of the connective tissues and blood channels causes atrophy of the tubule

Fig. 9. Section of stomach epithelium, connective tissue and a portion of the digestive gland. The large dark bodies are the "pigment" cells filled with coarse granules of (natural) yellow color. Numerous parasites are present with the usual concentrations of leucocytes and fibroblasts. The tubules of the digestive gland show the characteristic shrinkage of the epithelium. Heidenhain's haematoxylin and eosin. Magnification about 220 diameters.

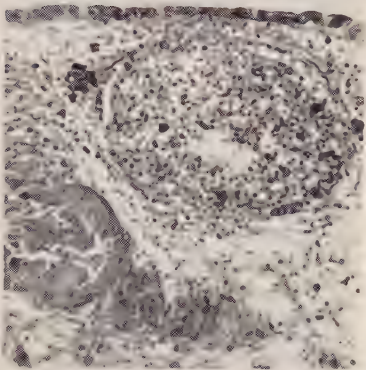
Fig. 10. Margin of an abscessed mantle. A characteristic abscess is against the epithelium and contains massed parasites, tissue debris, and leucocytes. Several smaller abscesses are shown also, which are filled with the peculiar basophilic-staining fluid also shown in Fig. 8. Parasites are not confined to the abscesses; they are distributed throughout the surrounding connective tissue but in smaller numbers. Delafield's haematoxylin and eosin. Original magnification about 220 diameters.

Fig. 11. Abscesses in the mantle. The epithelium over one of these has disintegrated and that portion remaining is necrotic. "Pigment" bodies and fibrous tissue are also shown. Delafield's haematoxylin and eosin. Original magnification about 220 diameters.

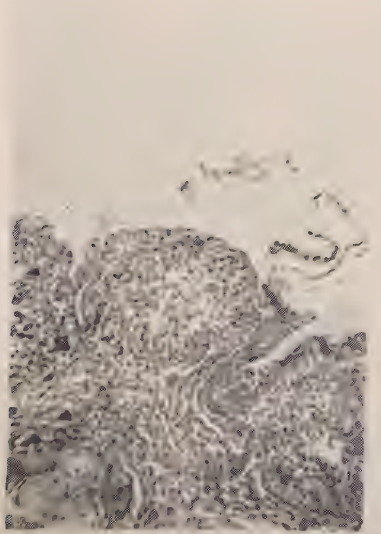
Fig. 12. Section of a portion of mantle showing almost continuous layer of necrotic abscesses under the epithelium, and in the center the mantle artery containing large concentrations of parasites in the walls and lumen. Against one end of the artery is a large nerve trunk. The usual fibrosed condition and "pigment" bodies are shown. Note the large number of parasites in the lumen of the artery. Delafield's haematoxylin and eosin. Original magnification about 100 diameters.



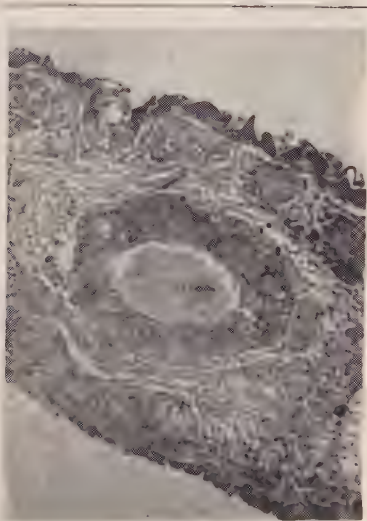
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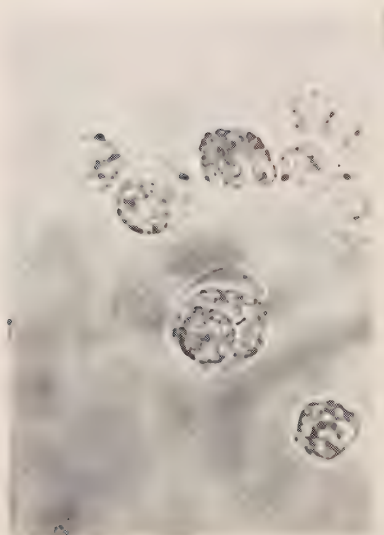
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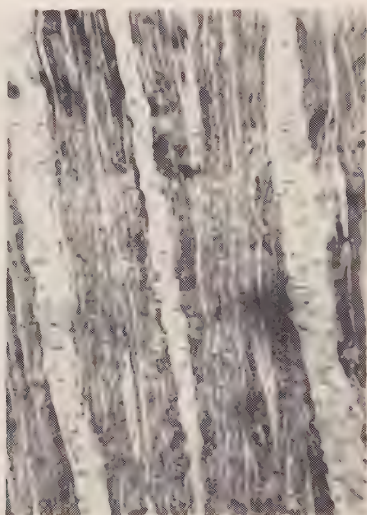
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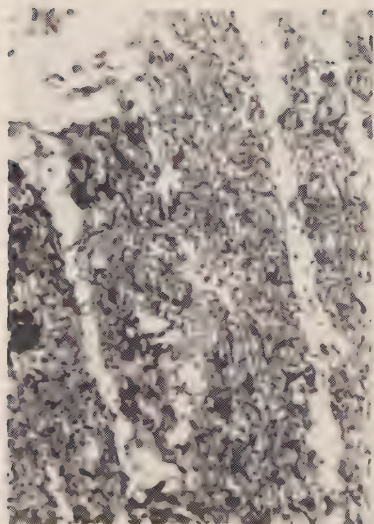
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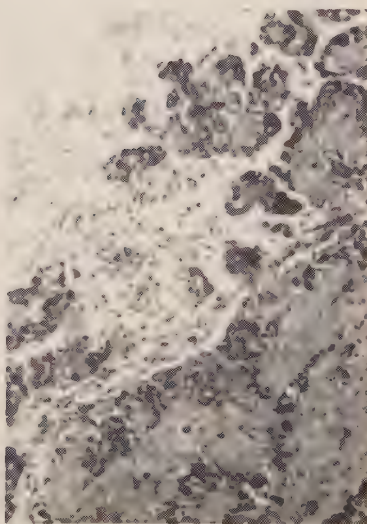
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epithelium which ends in necrosis of the cells. Compare Figure 6 which shows normal tubules, with Figure 9, a heavily infected tissue.

Peripheral nerves are seldom penetrated by *D. marinum* even when concentrations of parasites may be heavy around the bundles (see Fig. 12, nerve at one end of oval blood vessel). A special study of the visceral ganglion however, shows that this primary nerve center is often invaded, especially in the cortical layer containing the nerve cell bodies or neurons proper. Small abscesses occur in this layer with complete destruction of nerve cells (Fig. 16).

Considerable study of the effects of *D. marinum* infection on development of gonadal tissues has been made. Because of the great interest in this phase of the matter and the considerable data involved, this part of the investigation will be presented in a later paper.

DISCUSSION. While much remains to be done in analysis of effect of *D. marinum* infection of oysters, certain broad points of interest are apparent. The first of these is that the disease has several points of similarity of effect to certain generalized mycotic infections in man. The fact of susceptibility of nearly any tissue to invasion is distinctly like fungus infections of the type of histoplasmosis and North American blastomycosis. Widespread involvement of various organs and tissues without development of acute toxic symptoms, and steady progressive development, are characteristic of the human mycotic diseases in which the infective element is a spherical yeast-like cell not develop-

Fig. 13. Moribund leucocytic cells from the pericardial cavity of a gaper. The tissue debris from disintegrating cells is also characteristic. *D. marinum* cells are contained in the leucocytes. Original magnification about 950 diameters.

Fig. 14. Longitudinal section of bundles of muscle fibers from the adductor muscle of a normal, uninfected oyster. The blood sinuses are traversed by a light fibrous tissue. Note length of normal fibers as shown by several in contraction. Delafield's haematoxylin and eosin. Magnification about 220 diameters.

Fig. 15. Lysis and destruction of a heavily infected portion of adductor muscle. Original location of two blood sinuses may still be seen. Note irregular masses of short sections of fibers disconnected from each other. Delafield's haematoxylin and eosin. Original magnification about 220 diameters.

Fig. 16. Section of the margin of the visceral ganglion of a heavily infected gaper. The darkest cells are neurons. An abscessed area containing numerous *D. marinum* cells has cut through the cortex and a few scattered parasites may be seen in small lysed cavities deeper in the medullary portion of the ganglion. Delafield's haematoxylin and eosin. Original magnification about 220 diameters.

ing mycelia in the host. In addition to those named above, South American blastomycosis, cryptococcosis, coccidioidomycosis and rhinosporidiosis belong in the same category. This is not a suggestion that mycotic infection of man may result from *D. marinum*; there are no data to indicate such relation.

The capacity of *D. marinum* to build up massive infections before death of the host is also of interest. This would seem to indicate that the association of the two species may be of long standing, allowing as it does to both host and parasite a period of reproduction before infection destroys the host. While the exact percentages of infection for oysters of less than one year have not been worked out as meticulously as have those for older oysters, it has been obvious from the beginning that such younger individuals are not infected to the extent that older market size individuals are. It is not believed that this is a physiological difference in susceptibility, but probably is a result of the mechanics of infection. However, oysters in Louisiana under one year of age are vigorously reproductive and as far as interrelationship of species is concerned there seems to be a successful adjustment between parasite and host. This adjustment has not been carried to the point of tolerance, by individual hosts, of heavy infection, indeed there seems to be no effective physiological brake, in the form of immune reaction, to the progressive lysis of entire organs and systems.

In conclusion, the tendency of *D. marinum* infection to produce multiple abscesses in varied tissues is of interest. A study of the literature of oyster mortalities shows that abscess production is one of the common denominators wherever sufficiently minute observations have been made. The studies of Giard (1894), Needler and Logie (1947), and Roughley (1926) are cases in point. It is not being suggested that *D. marinum* is the etiological agency in those cases, but that the waves of shellfish mortality in general may often be produced by organisms of similar physiological nature and that the preponderance of effort devoted by biologists to environmental measurement without correlated pathological studies may be misdirected.

SUMMARY

A study of the histopathological effects of infection of oysters by *Dermocystidium marinum* shows that the early stages are characterized by inflammation followed in turn by fibrosis and extensive lysis of the tissues. Under conditions of high temperature and high salinity

massive infections develop, involving all tissues but producing most extensive damage to connective tissues, adductor muscle, digestive epithelium and blood vessels. Attention is called to the resemblance of this type of infection to certain mycoses of man.

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